THE

NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.R.S.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

IN CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

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INDEX OF SUBJECTS.

INDEX OF AUTHORS.

ERRATA.

Vol. XIX, Nos. 7 & 8.

Page 202, line 5 from bottom and in second footnote, *for* K *read* K_1.

Page 203, line 12 from top, *for* it *read* r.

Page 204, line 13 from top, *for* $\frac{R}{100} = \frac{W_2 - W_1}{W_1}$ *read* $\frac{R}{100} = \frac{W_2 - W_1}{\frac{W_1 + W_2}{2}}$

" line 15 from top, *for* $\frac{\frac{L_1 + L_2}{2}}{W_1}$ *read* $\frac{L_1 + L_2}{W_1 + W_2}$

" line 7 from bottom, *for* $\frac{L_2 - L_1}{L_1}$ *read* $\frac{L_2 - L_1}{\frac{L_1 + L_2}{2}}$

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THE EVOLUTION OF PLANTS.

NO such interesting theoretical contribution to a subject which is of primary interest to all botanists, and indeed to all biologists, as that recently published by Mr. Church,[1] has appeared for many years. It is impossible to attempt in the limited space available a comprehensive review of the theses and arguments developed by the author, even if any one botanist had the necessary competence, for there is scarcely an important biological problem which Mr. Church does not raise. All we can do here is to call attention to some of the fascinating expositions and speculations of the author, and indicate certain points of possible criticism. At the same time we would strongly recommend all botanists to obtain and read this work for themselves. It is rather hard reading, for the author's style is none too easy. He has a fondness for long and rather involved sentences, but he never fails to arouse interest and to stimulate thought and imagination. The price, in these days, is almost ridiculously cheap; for the same matter, printed with wider spacing and on a smaller page would easily fill a fair-sized volume. The work contains in fact about 60,000 words, more or less—the length of an ordinary "six shilling" novel, now costing seven shillings, at just half the price—while to the biologist it is more entertaining, and much better worth reading than most novels. Though often involved, the style is lively throughout, and Mr. Church's castigations of those who have had the misfortune to express opinions with which he disagrees, or to take what he considers a narrow view, to see the subject "out of perspective," never fail to amuse. The author's polemic, though often expressed in the language of almost contemptuous scorn, has the happy quality of leaving no poisoned sting behind. And this, though the author

[1] A. H. Church. *Thalassiophyta and the Subaerial Transmigration.* (Oxford Botanical Memoirs, No. 3), pp. 95, 3s. 6d. net., Oxford University Press, 1919.

is not always fair to those he criticises, occasionally misrepresents them, and is not infrequently slightly irritating to the reader, by reason of his air of Olympian detachment.

The first thesis is that just as the higher land plants have inherited their fundamental cell mechanism from primeval phytoplankton, so they have inherited the external form and segmentation of their bodies and the most fundamental tissue differentiations from phytobenthon, *i.e.* from fixed, branching and leaf-bearing seaweeds, with radial organization, "Fibonacci" sequence of members and apical meristem. The author regards as inconceivable the idea that land plants have produced an equipment so parallel to that of marine algæ, as leaf and stem, parenchymatous tissues and radial organisation, in response to conditions so different from an aquatic environment as those of subaerial life. As a working hypothesis of evolution "the antithetic theory," he says, "is better than nothing at all; and for fifty years[1] it has dominated the botanical outlook (1851-1908) and has afforded an effective stimulus to research. The only effective criticism is the establishment of an alternative point of view; and those to whom the surprising adventures of an intercalated 'post-sexual phase' may not appeal, are naturally expected to provide something more rational." There have been many to whom these "surprising adventures" have made no appeal, nor have there been wanting attempts to present "an alternative point of view"—one was published in this Journal in 1907—though no doubt they were poor things beside the magnificent sweep of Mr. Church's exposition.

The author then proceeds to explain how the antithetic theory of alternation was rooted in the course of development of botanical research in the middle of the nineteenth century. "To Hofmeister, working at Leipsig and Heidelberg, in ignorance of the Sea, the progression of plant life was viewed from the *standpoint of the freshwater pond*, and in the light of a transition from the medium of fresh water and seasonal vegetation to the arboreal vegetation of the North Temperate zone, as displayed in Central Europe." The contempt for marine algæ shown by so eminent a biologist as Schleiden in 1849 is well brought out by a

[1] Though in a certain sense broadly true this statement is open to criticism. Hofmeister's doctrine was not specifically antithetic. The antithetic doctrine began with Celakovsky (1868), and gained no widespread acceptance till Bower's paper of 1890 gave it a definitely evolutionary significance. Nor has the antithetic theory dominated the botanical outlook unchallenged. Cf. Scott (1896).

quotation from the "Grundzüge." But it should be noted that while this ignorance of the rich and marvellous vegetation of the sea by the "land botanist" may explain the absence of any serious attempt to go to seaweeds for light on the evolution of land plants, it has nothing to do with "antithetic" as opposed to "homologous" alternation. The author ignores Pringsheim (1856, etc.)

The second thesis is that there is no probability of plant life having migrated from the sea to the land, viâ estuaries and rivers to freshwater swamps, and that the origin of land plants from marine forms took place by what the author calls *transmigration*,[1] *i.e.* the slow emergence of land from the sea, carrying with it a plant population. The migration viâ inland waters the author thinks impossible because of the deficient food supply in the form of salts, and he points out that all freshwater algal vegetation is in fact diminutive in size (starved and stunted) as compared with that of the sea. The diminished food-supply of such habitats would lead to a serious diminution in output of reproductive cells and hence in failure to compensate the wastage of the race, and to ultimate extinction. Only inferior (unicellular and filamentous) forms could survive under such conditions, and we must look for the ancestors of the main land vegetation among massive forms comparable with the best equipped modern seaweeds.

In considering the possibility of the transformation of a massive seaweed into a land plant we have first to envisage the actual change of conditions involved, in their effect on the vegetative economy, the day-to-day life of the plant. First of course we have the localisation of water supply and of the supply of the essential elements of the "food salts." Of these the second is by far the most insistent, since the author calculates that over 150 litres of sea water would have to be passed through the plant in order to obtain sufficient nitrogen to make one gram of aqueous plasma (taking the nitrogen content of the sea—the original nutritive medium—as one part in ten million). This proportion of water to combined nitrogen, however, is progressively decreased as we pass to soils containing more humus. "A progressively sub-saturated atmosphere with attendant desiccation, now appears as a blessing in disguise," as enabling the plant to get rid of this enormous quantity of excess water, at the same time stimulating the flow of the current. Meanwhile increased insolation, and increased facility of gaseous exchange, immensely

[1] The fitness of this word to express the hypothetical phenomenon in question is not very clear.

overstimulates the formation of carbohydrate, which cannot be used in building new protoplasm because of the limited supply of the necessary food salts, and thus leads to the deposition of immense quantities of waste polysaccharide—a condition which reaches its extreme in tree trunks and in the thick walled tissue of xerophytes generally. The change to subaerial land life, in fact, while immensely facilitating gaseous exchange[1] and therefore the constructive processes depending upon it, severely restricts the formation of new protoplasm, which can only be carried on by absorption of a great excess of water, so that the body of a land plant is much more largely composed of dead substance than is that of a submerged seaweed.

"The algæ of the transmigration," says the author, "may be roughly visualised as having possessed the metabolic efficiency of the Chlorophyceæ, the somatic equipment [parenchymatous structure and body segmentation] of the Phæophyceæ, and a reproductive scheme of life history more advanced than that of *Dictyota*, though in other respects falling behind that of the modern Florideæ, in that these last have eliminated the flagellated zoïd as microgamete in favour of a simple method of spermatogamy. The algæ of the transmigration may be thus said to have combined the best features, as factors of the highest grade of progression, of the known great conventional series of marine phytobenthon, and yet to have belonged to none of them."

Mr. Church conceives of the condition for the evolution of such forms in the slow rise of the sea bottom to benthic conditions, *i.e.*, to within range of light penetrating from the surface. Thus emerges the conception of a *benthic* or *seaweed epoch* of the world's history, which followed upon the earlier *plankton epoch* in which the ocean covered the surface of the globe to a uniform depth.[2] In the benthic epoch marine vegetation culminated in the shallow water areas of incipient continents. The marine benthon existing to-day, rich as it is in variety and development, is regarded as being a mere impoverished remnant of the benthic age, since it is confined to restricted portions of the very narrow *littorals* of the continents, and, together with the great bulk of the forms of the benthic age, the actual ancestors of the land plants have completely disappeared.

[1] Mr. Church is under the impression that the transmigrant to subaerial life is under *worse* conditions for obtaining carbon dioxide than a water plant. He seems to have got his data on the rate of diffusion wrong.

[2] That the ocean ever did so cover the globe must be regarded as questionable.

Later on the conditions for the evolution *en masse* into land plants of the green highly developed benthon whose characters have been indicated were presented by the rise of the incipient continental areas above sea level. The land thus first exposed was not covered by more or less deep deposits of soil, the results of long continued subaerial denudation, but consisted of bare rock surfaces, bearing, according to the theory, great masses of marine vegetation. Copious precipitation and a saturated atmosphere may be reasonably postulated, but the supply of nutritive salts, supposed to be present in the primeval ocean, would be entirely cut off, unless we postulate a low tide-wave with periodic return, or wetting within the range of the "splash."[1] The emerging surface would however shortly be covered with the remains of dead forms which had *not* survived the first stage of the transmigration, and the organic débris so produced would form the first (an organic) soil, from which the soil as we know it would be evolved by the gradual accumulation of the products of subaerial denudation. This organic débris would remain saturated in a saturated air, and would furnish the substratum from which the transmigrants would have to obtain their food.

And now we come to the weakest part of the author's exposition—his account of the way in which the vegetative bodies of these transmigrants became actually adapted to land life. Admitting that his general considerations are sound, and that his analysis of the factors is correct, we find no convincing picture of the actual transformation. Mr. Church conceives that the various types of algal organisation originating in the sea maintained their essential characters after the transmigration. Plankton forms remained plankton, even if they became "cryoplankton" or "dendroplankton": filamentous forms remained filamentous; and the more massive parenchymatous forms retained their cellular organisation which formed a basis for further adaptation. Thus we have the picture of comparatively massive forms capable of standing up by themselves (comparable with the Fucaceous *Cystoseira*) having an initial advantage on this account and being able by their massive structure to resist desiccation; increasing their deposits of "polysaccharide" (cellulose) as a result of the greater insolation;

[1] Here it may pertinently be asked: What is the probability that the primeval ocean had anything like the salt content of the sea as we know it to-day? The *original* ocean must have consisted of water condensed and recondensed on the cooling surface of the globe, and thus destitute of salts. How and when did it acquire its existing salt content?

initiating a subaerial "balancing mechanism" (geotropism); starting a root system by the boring down into the organic débris of the substratum of the massive "crampon system" (such as we see to-day in *Fucus* and *Turbinaria*) with vestiges of the "trichome system" surviving as root hairs; and a stele by lignification of the central cells of the axis, the peripheral "phloem" and secondary meristematic activity being already indicated among the massive brown seaweeds. This is all very well, but it is extraordinarily difficult to visualise exactly how, and by what stages it happened and the author gives us little help in this respect.

In writing of reproductive structures in relation to the transmigration Mr. Church is particularly interesting. He regards the archegonium as "clearly an end-product of oogamic evolution, the limiting term of something quite unknown, probably originating in something quite different from any recent archegonium, and, if we saw it, scarcely recognizable as such," "very probably of polyphyletic origin." He points out that in so far as the archegonium is a means of obtaining fertilization *in situ* for an oosphere, whose post-sexual nutrition involves a parasitic diploid embryo, it shares these characters with the egg-bearing organs of Florideæ, and hence such phenomena are part of the reproductive equipment evolved in the sea. The origin of the archegonium, as we actually know it, must therefore be sought in the transmigrant phyla, as a result of adaptation to the new conditions. But if, the author argues, fertilisation *in situ* had been developed *during* transmigration, the archegonial "oospore" would have been utilised as a resting phase, as happens in the transmigrants *Chara*, *Vaucheria*, etc., whereas in fact it always develops directly.

The origin of the archegonium and of the antheridium he seeks in a multicellular branchlet of the algal body, represented in the Phæophyceæ by the "multilocular" gametangium, thus following the line indicated by B. M. Davis (1903), though Church insists on the importance of the distinction between the algal gametangium liberating autotrophic zoïds and the antheridium of Archegoniates, whose zoïds have to be fed as well as protected from desiccation during development. Added to this we have the further transmigrant mechanism of dehiscence by turgescent terminal wall-cells on supply of free water. Church calls attention to the "primitive" features of the archegonium of *Sphagnum*, the most alga-like moss, and develops the analogy of the archegonium with the female organ of *Chara*, a transmigrant which tried to solve, with

indifferent success, the same problem that the Proto-archegoniate solved satisfactorily. The "exaggerated" neck of the archegonium the author compares with the pseudostylar micropyle of certain Gymnosperms and the stylar tube of Angiosperms.

Thus the essential features of the archegonium and of the antheridium appear an evolution of a multicellular fertile algal branchlet (the first beginnings of which appear in *Dictyota*), in response to the conditions of subaerial life, obtaining incidentally the advantages of the oogamy and of fertilisation and development *in situ*, advantages which the Florideæ (and *Chara*) in part have obtained in other ways.

The archegonium is polyphyletic in origin, and never existed in a condition of completely submerged algal benthon. Not only the Bryophytes but also different phyla of Pteridophytes are to be traced back to distinct origins, not only among marine benthon, but to distinct flagellate plankton ancestors. This conclusion was already suggested by the work of Bohlin and Luther (1897-1901) on the zoospores of algæ, though few students of the Archegoniatæ have been bold enough to follow out its full consequences, which involve the derivation from distinct flagellate types, not only of Ferns and Lycopods but also of Equisetales, and perhaps of *Isoëtes*, though the octokont zoïd of this genus may be derived from the isokont type. The whole trend of modern morphological investigation, indeed, encourages us not to be afraid of postulating far-reaching extension of independence of origin with convergence and homoplasy; and such postulates may justifiably be carried to a point which would have scandalised the older morphologists.

The origin of the archegonium and antheridium is only one problem raised by a consideration of the evolution of the reproductive mechanism of the green land plants. The sporogonium of the Bryophyte Mr. Church regards as the reduced form of a benthic radially organised shoot, from which, he thinks, the leaves have disappeared, leaving the photosynthetic mechanism on the axis. He strongly upholds Bower's contention that radial organisation is primitive, and insists that it originated as a response to the benthic conditions of life, since it is the common type among seaweeds. Dorsiventrality in land plants, for instance in the dichotomous dorsiventral liverworts, he regards as an evidence of degeneration or perhaps of derivation from degenerate dorsiventral seaweeds. The photosynthetic and transpiratory structures of sporogonia must either have been evolved independently of the corre-

sponding structures in the leaves of the sporophytes, or be regarded as relegated to the axis when the leaves of an originally leaf-bearing sporogonium disappeared. The latter hypothesis, to which Mr. Church inclines, seems gratuitous. Why should the leaves have disappeared completely leaving no trace? Is not the hypothesis of independent origin of the photosynthetic mechanism both simpler and fully justified on the general principle of homoplasy?

The "immersed" archesporium of the sporogonium (and equally of the sporangia of Pteridophyta) is to be taken as a layer of potential tetrasporangia, a tetrad being the characteristic limiting term of the benthic unilocular sporangium in which the meiotic mechanism determines the number four. Such immersion is commonly met with in the stichidia of the bulkier Florideæ, and the later complications of the central portion of the axis (columella) and of the peripheral "wall" found in the larger sporogonia of the mosses, are merely further modifications, while degeneration is illustrated in the smaller forms culminating in the simple sporogonium of *Riccia*. In the Pteridophytes "the view of a continuous stratum of archesporial cells being normal for older fern-laminæ, followed by the progression of sorus-restriction, and the localization of smaller patches to a system of more elevated out-growths (sporangia), as secondary emendations for wind-dispersal," forms part of Bower's account of the evolution of the sporangium. But the aerial wastage of spores is far greater than the marine wastage—Mr. Church estimates it in *Aspidium* at about 1000 times that of the Laminarian—and to meet this the spore-producing surface increases vastly in bulk, culminating in the tree ferns (*Alsophila*, up to 60 feet high).

This enormous wastage is quite overcome in the heterosporous forms, where spore production is brought into immediate relation with the production of gametes already economised by the archegonial mechanism; and the prothallus, which through its precocious juvenile sexuality is already far more efficient than the large sexual plant as a means of obtaining quick returns in the reproduction of the race, is still further economised, and the necessary duration of its life shortened, by inclusion in the spore. The culmination of this process in the seed plants, where there is no wastage at all of sexual cells as such, and a minimum of wastage of microspores (pollen grains) and thus of male gametes when the insect pollination mechanism is brought to the greate pitch of perfection, is familiar ground.

On the broadest biological grounds, Mr. Church thinks the plant kingdom should be classified as follows:—

Thalassiophyta	Plankton. Benthon.
Xerophyta -	Xerophyton.

Xerophyta include not merely land plants but all plants which have a "water problem" in their economy and all freshwater forms which have survived the subaerial transmigration, to grow as best they can in media other than that of the sea.

Such, in very brief and incomplete outline, are some of the main features of Mr. Church's story of the evolution of the leading series of plant life on the earth. The outstanding feature of the story is the insistence on the large marine algæ as presenting us with various combinations of the factors, a selection of the best of which were employed in the adaptation to land life, and the corollary that only by a much more detailed and intensive study of seaweeds, can we obtain more positive knowledge of these factors. The characteristic merit of the author's contribution to the subject, is his insistence on the widest possible outlook, on a broad consideration, in the light of all the known facts, physical, chemical and physiological, as well as structural, of the necessary conditions of evolution of land plants from water plants. There can be little question that our view-points in comparative morphology have been too narrow and academic, and it is all to the good to be taken into a freer atmosphere. The writer may be forgiven if he finds in the stimulating atmosphere of Mr. Church's memoir one more evidence of the urgent necessity of escape from the bonds of our one-sided academic morphology in current teaching, and of laying far greater stress on a study of the physical and chemical conditions of life in its various forms. It is beside the point to reproach Mr. Church because he presents no new body of facts. He wants us to consider the facts we have in a saner manner, and to let the results of such consideration direct fresh research. Nor can we expect, as Mr. Church points out, to obtain fresh evidence on these points by searching for new fossils, exceedingly interesting as discoveries of new and simpler types of Pteridophytes, such as the recently described *Rhynia,* may be. It is overwhelmingly improbable that the original transmigrants which were the actual ancestors of our land flora have been preserved in fossiliferous rocks. We can only infer their characters, and that in the most general way, from a study of the structure and conditions of life of existing forms.

Once land plants were thoroughly established they must have acquired the general characters with which we are familiar, and the evidence of this or that variant on the type—one among thousands that must have existed—can tell us nothing significant about the general problem.

There are some points in Mr. Church's story that are doubtful or obscure. For instance he postulates a uniform ocean two miles deep on the surface of the earth as the medium in which the plankton phase of life was evolved and developed its perfection. The benthon age was made possible only by the approach of the sea bottom to the surface of the water as a preliminary to the emergence of continents. Geophysicists are not however agreed that this was the course of events. Some hold that there may have been land surfaces before the world was cool enough to support life. The "orthodox" biological view is that life arose in the warm water along the littoral and not as plankton in a uniform ocean. Unless we have a sound physical basis for the belief in the existence of a uniform ocean before land appeared the hypothesis of a plankton age preceding the benthon age is not necessary. Life may have originated as plankton, but we cannot be certain a priori that it did. There is also the question of the history of the content in mineral salts of the water of the primeval ocean.

We shall be glad to publish criticisms or remarks on the subject of Mr. Church's memoir, which raises, as was said at the outset, so many questions of the first biological interest.

A. G. T.

PHYLOGENETIC CONSIDERATIONS ON THE INTERNODAL VASCULAR STRANDS OF *EQUISETUM*.

BY ISABEL M. P. BROWNE.

[WITH SEVEN FIGURES IN THE TEXT].

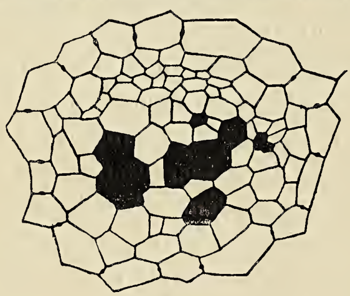
THE descriptions in the text-books of the vascular strands in the internodes of *Equisetum* are somewhat meagre and inadequate. In discussing the structure and nature of these strands it will be convenient provisionally to use the word bundle for them individually, without thereby prejudging their morphological nature.

Campbell (5, p, 464) figures such an internodal bundle of the aerial shoot, probably of *E. maximum*, Lam., for in the figure are to be seen the conspicuous tannin cells characteristic of this species. His drawing shows very clearly not only the carinal canal, with the remains of the carinal group of protoxylem adhering to its margin, but also the two lateral groups of metaxylem, situated near the periphery of the bundle and separated from the carinal canal by five or six cells. Curiously enough, his description makes no mention of these lateral groups of metaxylem. A rather fuller account of the internodal vascular bundles, including a description of the well-known carinal group of protoxylem and the two separate lateral groups of metaxylem, was given by Professor Bower (p. 386 [1]) in his *Origin of a Land Flora* in 1908. Professor Bower in his description and discussion uses the word axis and of his three figures of internodal bundles, copied from Pfitzer in Rabenhorst's *Kryptogamen-Flora*, two are from the rhizomes of *Equisetum litorale*, L., and *E. silvaticum*, L., and the third from the aerial stem of *E. palustre*, L. His description, though brief, is thus a general one. It may perhaps be pointed out that the words internodes of the axis cover a wider field than that to which Professor Bower's description applies. The bundles of the subterranean tubers and those of the primary axis are also, in part of their course, internodal axial bundles and Professor Bower's description is inapplicable to them.

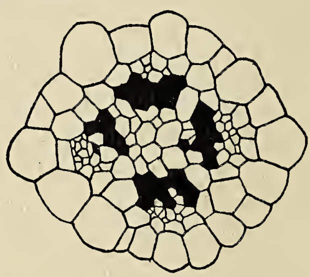
Subterranean tubers have been recorded from several species, and figures of their vascular bundles have been published for *E. arvense* by Milde (12, Pl. 1, Fig. 22) and by Ramey (15, Pl. 6,

[1] The small white space in the metaxylem-group on the reader's left is an intercellular space, not a parenchymatous cell.

Fig. 3), for *E. maximum* and *E. silvaticum* by Leclerc du Sablon (11, Figs. 15 and 17), and for the fossil *Equisetum* (or *Equisetites*) *stellare* Fritel and Viguier, from the Sparnacien by Fritel and Viguier (8, Text-Fig. 5 and Pl. IX, Fig. 3). Text-Fig. 1 *a* represents such a bundle of the tuber of *E. silvaticum.* It is copied from Leclerc du Sablon and the xylem is shown in black, in order to bring out its distribution more clearly. Except those of *E. arvense,* all the bundles of tubers that have been figured show essentially the same irregular distribution of tracheides, interspersed with small groups or bands of parenchymatous cells, though in the bundle of the fossil *Equisetites stellare* the cells, vascular and parenchymatous, are more numerous. According to Milde's figure the bundle of the tuber of *E. arvense* is also of this type, but in Ramey's figure of such a bundle the xylem consists of a solid group of 16 thick-walled tracheides.



a.



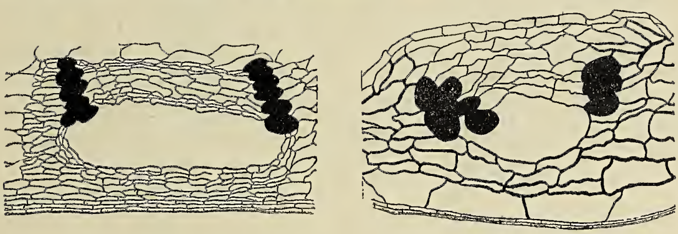
b.

TEXT-FIG. 1. (*a*) Transverse section of a vascular bundle of a tuber of *E. silvaticum,* after Leclerc du Sablon. Magnification not stated. (*b*) Transverse section of the third internode of the primary axis of *E. maximum,* er Buchtien. $\times 216$.

In the internode of the primary axis the xylem of each bundle forms a single group. This is shown in Text-Fig. 1 *b.*, representing a transverse section of an internode of the primary axis of *E. maximum,* Lam. The figure is copied from Buchtien (4, Pl. 5, Fig. 119) and again the xylem has been filled in in black. The wood of each of the small bundles consists of five to ten, on average of eight tracheides. In the more reduced bifascicular primary axis of *E. variegatum,* figured by the same author, each bundle contains four or five rather small tracheides, irregularly embedded in parenchyma (4, Pl. 5, Fig. 118).

But even in the internodes of the aerial stems of *Equisetum* the structure of the bundle is not always uniform. For the two postero-lateral groups of metaxylem are not always separated from the more deeply-seated carinal group of protoxylem. A study of

Milde's figures of the internodal bundles of the aerial stems shows tha in *E. mexicanum*, Milde, *E. Schaffneri*, Milde and *E. lævigatum*, A. Braun the lateral bands of metaxylem abut on the carinal canal and are, therefore, in connection with any of the earlier-formed tracheides which may persist at the edge of the carinal canal. Text-Fig. 2 *a.* and *b.*, adapted from Milde (12, Pl. 23, Fig. 7 and Pl. 32. Fig. 5) show this condition in the two last mentioned species. Milde's figures of similarly situated bundles in *E. Martii*, Milde and *E. giganteum*, L., though unsatisfactory, because drawn on a very small scale, seem to show that in these species also the lateral bands of metaxylem are, sometimes at least, in contact with the canal resulting from the disorganization of the first-formed tracheides (12, Pl. XX, Fig. 3, and Pl. XXI, Fig. 4). Again, Milde's figures of the internodal bundles of the aerial axes of *E. xylochætum*, Mett. and *E. debile*, Roxb. show that in these species one of the lateral groups of metaxylem may come into contact with the edge of the carinal canal, while the other may



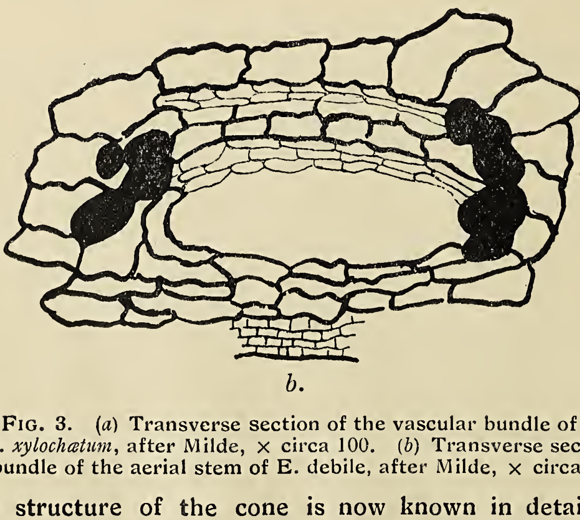
a. *b.*

Text-Fig. 2. (*a*) Transverse section of the vascular bundle of the aeria stem of E. *Schaffneri*, after Milde, × 176. (*b*) Transverse section of the vascular bundle of the aerial stem of *E. laevigatum*, after Milde, × 176.

remain separated from it either by a single parenchymatous cell or by a few such cells. Text-Figs. 3 *a.* and *b.* are adapted from Milde's figures of such bundles in *E. xylochætum* and *E. debile* respectively (12, Pl. XIX, Fig. 8 and Pl. XXVI, Fig. 17). Quéva (14, p. 23) has remarked that in *E. litorale* Kühlew the vascular bundles below the node assume a remarkable appearance owing to the linking up of the lateral bands of metaxylem at the edge of the carinal canal. His figure 21 shows that this species possesses locally a bundle which is essentially similar to the types of bundle depicted in Text-Fig. 2 and 3. Text-Fig. 4 *a.* is from a preparation of one of the upper internodes of the cone-bearing stem of *Equisetum giganteum.* The lateral groups of metaxylem are here almost in contact with the carinal canal; between them lies an irregular band of tracheides, broken in the middle and on one side

by parenchymatous cells; the band is roughly parallel to the carinal canal. This figure illustrates the fact that there is some variety in the way in which the lateral metaxylem groups approach or become linked up with the carinal group; in some cases they first approach one another.

a.



b.

Text-Fig. 3. (*a*) Transverse section of the vascular bundle of the aerial stem of *E. xylochætum*, after Milde, × circa 100. (*b*) Transverse section of the vascular bundle of the aerial stem of E. debile, after Milde, × circa 460.

The structure of the cone is now known in detail in four species, *viz.*, *E. arvense*, L., *E. palustre*, L., *E. limosum*, L., *E. maximum*, Lam. In none of the cones of these species do the

vascular bundles of the internodes[1] show a separation of the xylem into three distinct groups. In the internodes of the cones of all these species (Browne 2 and 3) the vascular tissues may be disposed in single separate bundles—*i.e.*, in strands which at the node above give off the vascular supply of one sporangiosphore—or in bands giving off at the next node, traces to two or more sporangiosphores. As the vascular strands in the internodes of the vegetative axes are always single bundles it will be convenient in the subsequent discussion to select single internodal bundles of the cone rather than bands for comparison with other internodal, axial bundles. The structure of the bands is similar in essentials to that of the single bundles, but the former are, naturally, considerably wider than the latter.

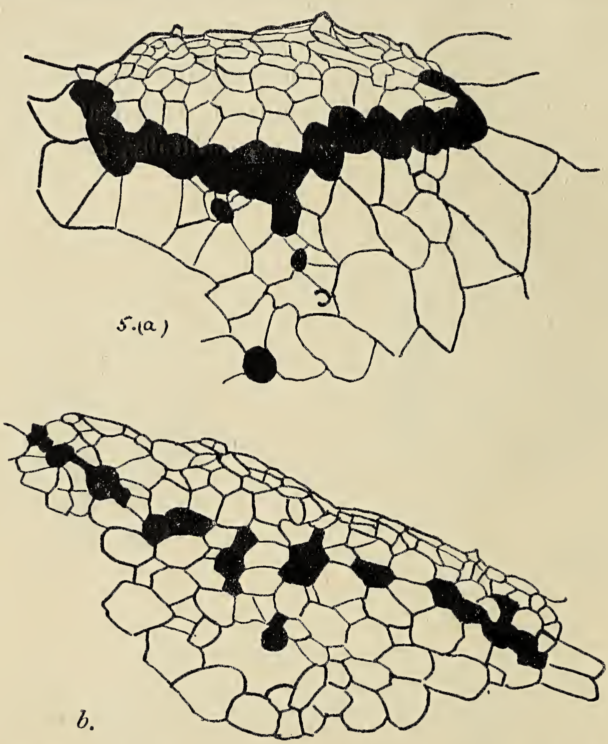
a. *b.*

Text-Fig. 4. (*a*) Transverse section of small vascular bundle of upper part of fertile stem of *E. giganteum*, × circa 250. (*b*) Transverse section of small vascular bundle in one of the internodes of the cone of *E. giganteum*, × circa 325.

Text-Fig. 5 *a* represents such a bundle, rather a small one, just below the lowest whorl of sporangiophores in *E. arvense*. Except that higher up the slight outward concavity of the xylem is replaced by a slight inverse curvature, so that the band of xylem conforms to the curve of the periphery of the stele, and that there is, in the example figured, a single large, possibly centripetal tracheid in the pith internal to the carinal canal, this bundle is

[1] The words internode and internodal bundles are here used, for convenience sake, to denote the axis of the cone between the sporangiophores and the bundles at levels where the latter are not giving off traces. The use of the term is not intended to imply a true homology between a vegetative node and the axis of the cone at the insertion of the sporangiophores, since this depends upon the undecided and highly controversial question of the morphological nature of the latter.

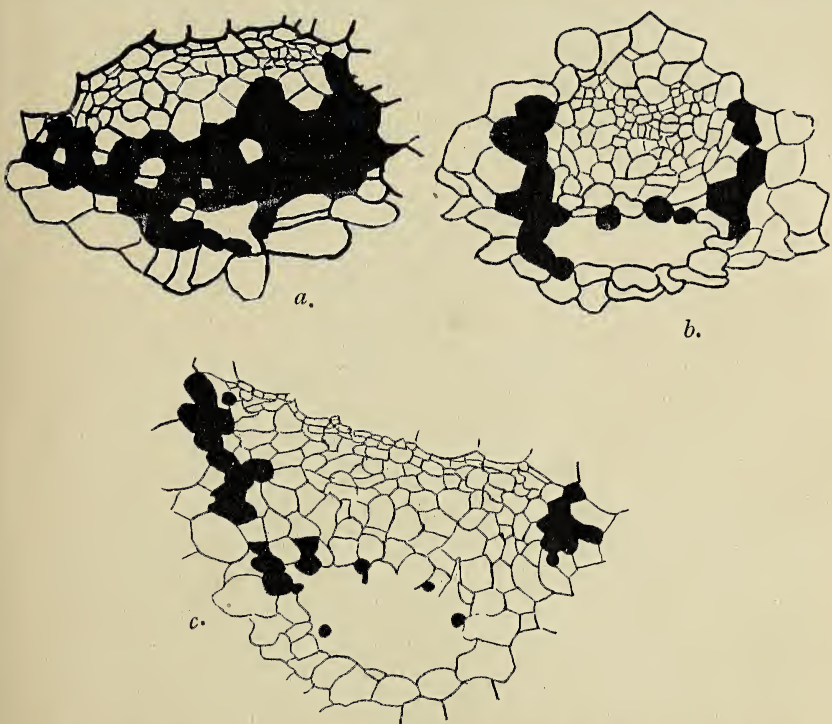
quite typical of the internodal bundles of the cone. These bundles show considerable variations. Often the more or less transverse band of xylem is in contact with a small central group of tracheides slightly further in. Though there is usually no definite carinal canal the internal tracheides are often torn, especially towards the base of the cone. Often there are also other little groups of small tracheides internal to the main transverse band of wood and



Text-Fig. 5. (*a*) Transverse section of small vascular bundle of *E. arvense*, just below lowest whorl of cone, × circa 245. (*b*) Transverse section of small vascular bundle of *E. maximum*, just above the insertion of the annulus, × circa 250.

adherent to it or separated from it by a cell or two. The transverse band of xylem is typically one cell in depth, but locally it may be two or more cells in radial extent. It is often broken by a parenchymatous cell or small group of such cells. A markedly greater development of this interruption of the main band of tracheides is characteristic of the cone of *E. maximum*. Text-Fig. 5 *b*, though actually drawn from a bundle just above the level of the annulus, is quite characteristic of many cone-bundles. In this species the carinal canals, though decreasing in size, are often

persistent through the lower internodes of the cone. The bundles in the internode of the cone of *E. palustre* are very much like those of the cone of *E. arvense;* but though varying somewhat they are on average markedly narrower and their xylem tends to attain a very slightly greater depth radially. In the internodal bundles of the cones of *E. limosum* and *E. hiemale* the xylem is of no greater radial extent than in the similarly situated bundles of *E. arvense*, and the bundles themselves are, typically, quite as narrow as those of *E. palustre*. Those of *E. giganteum* have a considerably greater



TEXT-FIG. 6. (*a*) Transverse section of vascular bundles of *E. giganteum*, just below insertion of annulus, × circa 250. (*b*) Transverse section of vascular bundle of *E. giganteum* from axis just below the insertion of the annulus × circa 200. (*c*) Transverse section of small bundle of *E. arvense*, between the insertion of the annulus and the lowest whorl of sporangiophores, × 200.

radial depth of xylem, as may be seen in Text-Fig. 4 *b*, representing a small bundle of the internode of the cone of this species. In the fully developed bundle of this species the xylem is usually five to six, not uncommonly seven to eight cells in depth, so that the wood forms oval masses, sometimes broken up by or enclosing parenchymatous cells.

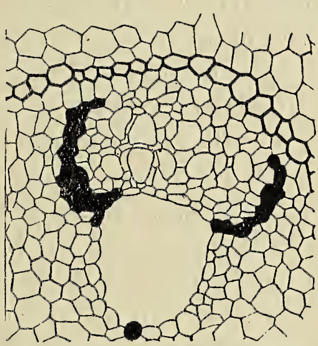
As a rule the transition from the bundle with two metaxylem groups to the type of bundle characteristic of the cone occurs a little above the annulus. In *E. giganteum*,[1] presumably correlated with the vascularization of the annulus, the change occurs a little below the insertion of the annulus; so that in this species the bundles just below the annulus much resemble the bundles of the internode of the cone (cf. Text-Fig. 6 *a*, of a bundle in this region with Text-Fig. 4 *b*). Usually the lateral bands of metaxylem become united with any persistent tracheides of the carinal group, and when this linking up is completed we get for a time a distribution of the xylem of the bundles recalling strikingly that found in the bundles represented in Text-Fig. 2 *a* and *b*. Text-Fig. 6 *c* shows a phase in this process in a bundle of *E. arvense*. Here one of the lateral groups of metaxylem has spread almost as far as the edge of the carinal canal, while the other has hardly increased in size or changed in outline. Text-Fig. 6 *b*, is of a bundle of *E. giganteum*, a little way below the insertion of the annulus, before the xylem has assumed the form characteristic of the internodal bundles of the cone.

We may now consider very briefly the structure of the bundles in the internode of the rhizome. So far as I have been able to ascertain, there is only one case recorded from the rhizomes of existing Equiseta in which the lateral groups of metaxylem show any approach to the carinal group of tracheides. Such an approach occurs, according to Quéva, in the rhizomes of *E. litorale* (14, p. 30), where the lateral metaxylem is only separated by a single cell from the protoxylem adhering to the carinal canal. It is by no means surprising that examples of bundles in which the lateral metaxylem is sufficiently well-developed to approach close to or to come into contact with the protoxylem are rare in the rhizome; for Quéva has shown that the metaxylem is generally less well developed in this region. Indeed, according to him, it may sometimes be completely wanting from the rhizomes of *E. maximum* and *E. limosum* (14, p. 30). Milde's figure of a part of the rhizome of *E. pratense* shows three bundles, one without any lateral metaxylem and two with a single metaxylem-tracheide on one side and none on the other (12, pl. VII, Fig. 9). Milde also figures a bundle without lateral metaxylem from the rhizome of *E. maximum* (12, Pl. IV, Fig. 1), though his figures of other bundles of the rhizome of this species show the lateral metaxylem

[1] The structure of this cone is more fully described in a paper soon to be published in the *Annals of Botany*.

quite well. The same author figures too a bundle of the rhizome of *E. silvaticum* in which the lateral metaxylem is represented by a single element on each side (12, Pl. IX, Fig. 9). According to Quéva there is often only a single element of metaxylem on each side of the bundles of the rhizomes in *E. maximum* and *E. limosum* (14, pp. 29-30).

In the only fossil rhizome of *Equisetites* the internal structure of which has been elucidated, that of *E. noviodunense*,[1] the elements composing the lateral bands of metaxylem are exceptionally numerous (in the bundle figured 11-17 in each band) and each group of metaxylem extends from near the periphery of the bundle to the edge of the carinal canal (8, Text-Fig. 7 and Pl. 9, Fig. 2). Text-Fig. 7 is copied from a schematic figure of such a bundle



TEXT-FIG. 7. Transverse section of the vascular bundle of the rhizome of *Equisetites noviodunense*, after Fritel and Viguier. Magnification not given.

given by Fritel and Viguier. As in the other Text-Figs. of the present paper the xylem is filled in in black.

Reduction of the lateral groups of metaxylem is not confined to the rhizome. Milde figures a bundle of the aerial stem of *E. trachyodon* in which one of the lateral groups of metaxylem is developed in a typical manner and the other is totally absent (12, Pl. XXXIII, Fig. 15). I have noticed that commonly in *E. limosum* lateral metaxylem is not present in the bundles for a part of the region lying between the last whorl of leaves and the annulus. Just below the level of insertion of the annulus, and on the breaking up of the nodal ring of wood, lateral metaxylem is present; but in the four cones of which I have made serial sections of this region it is absent from the bundles for a varying distance between these two points. In the anatomically very different cone of *E. giganteum* I have also observed in some cases the absence and

[1] The tubers described as *E. stellare* were probably born on the rhizome of this species.

in others the very poor development of the lateral metaxylem at this level. In this species, however, the lateral metaxylem groups may be well-developed over the whole of the region between the last whorl of leaves and the point, just below the insertion of the annulus, at which the xylem of the bundles assumes the more compact form characteristic of the axis of the cone.

We may now ask which among the types of internodal bundle found in *Equisetum* is the most primitive. These bundles belong to five principal types. The first, that with a solid mass of xylem, is found, so far as we know, only in some of the tubers of *E. arvense*; the second, in which xylem and parenchyma are irregularly intermingled in an oval or circular mass, is characteristic of some of the tubers of *E. arvense* and of all the tubers of other species the internal structure of which is known to us. Thirdly, there is the well known type of bundle consisting of a central protoxylem group and two postero-lateral groups of metaxylem. Then there is the form of bundle in which these two lateral groups are absent or very poorly developed. Lastly there is the type of internodal bundle in which the xylem is more or less continuous, though its outline varies. Often, especially in the aerial axis, the xylem-strand is U-shaped, with protoxylem at the innermost point. In other cases, *e.g.*, usually in the cone, the xylem represents the segment of a circle, often very narrow radially, and with one or more groups of small elements at or near its inner edge.

It seems clear that the tubers are modified rhizomatous branches, adapted for purposes of storage, and it can hardly be doubted that their bundles are cœnogenetic in character. They are interesting in that they show that the bundle consisting of three separate groups of xylem is not universal throughout the internode, even of the better known European species of the genus. It seems natural to regard the tubers as modified storage branches of the rhizome and their bundles as phylogenetic derivatives from the bundles of the rhizome. Duval-Jouve, indeed, has induced the production of branches below the whorl of leaves that forms a crown to the tubers. He found that if the tubers were grown in very wet earth they produce branches that grow into rhizomes; but that if grown in water and exposed to the light, the branches developed as aerial axes (6, p. 6—7). It is probably significant that though Fritel and Viguier give a list of eleven extinct, tuber-bearing fossil species of *Equisetum* (or *Equisetites*), the oldest being the Triassic *E. Mougeoti* Brgnt. and *E. arenaceum* (Jaeger) Bonn, yet no definite tubers have

been recorded from the characteristic palæozoic Equisetales, the Calamariæ. It is true that a few years ago Mr. Kidston (10) figured and gave a short description of what he termed a "rhizomatic tuber," belonging to an undetermined Calamite of Westphalian age. In this case, however, the tuber consists in three swollen internodes of a rhizome, the other internodes of which appear to be unaffected. This certainly seems a less specialized condition than the development of "chaplets" of tubers or of special branches as single tubers. It should noted that Duval-Jouve figures a rhizome of *E. arvense* in which a single internode is swollen and tuberous (6, Pl. I, Fig. 2).

Again, the type of bundle in which the lateral metaxylem is absent, or reduced to a cell, seems clearly to have arisen by reduction of the metaxylem from the bundle with three separate groups of xylem. Between this last-mentioned type of bundle and that with continuous xylem there exists, as has been shown above, a fairly complete series of intermediate forms. We can hardly doubt that one of these types has arisen from the other. Which, then, is the more primitive? The question is one of some importance, for, if the three groups of xylem have arisen in the phylogeny by the breaking up of a single mass of xylem, owing to the failure of certain cells to develop as tracheides, then the whole bundle is, as has been recently claimed by Eames (7, pp. 593-524), clearly a phylogenetic unit.

It seems to me that the arguments in favour of the priority of the bundle with continuous xylem are very strong. In the first place such priority would assume the gradual reduction of the bundle in the Equisetaceæ, and few, if any botanists, would now dispute the proposition that the existing species of *Equisetum* are reduced forms. There can be little question but that some of the Mesozoic *Equisetites* were among the ancestors of the recent genus *Equisetum*; and these mesozoic fossils show, on the whole, a diminution in size as we pass up from the older to the more recent rocks. Secondly, it is clear that in the rhizome the vascular tissues are, on the whole, markedly more reduced and it is here that we find hardly any indications of the continuity of metaxylem and protoxylem. I certainly regard it as significant that in the only fossil rhizome of which we possess a detailed anatomical account the lateral metaxylem is more highly developed than in the recent forms and is continuous with the protoxylem. This rhizome, known as *Equisetites noviodunense*, comes from the Sparnacien, and it would seem that at this geological horizon the reduction of the vascular tissues, even in the rhizome, had not

brought about the separation of the xylem of the bundle into three groups. Unfortunately the aerial axes of this species are unknown; but it seems probable that in them too the xylem of the bundle was continuous. A third argument in favour of the priority of the bundle with more or less continuous xylem over that in which the wood forms three separate groups, lies in the fact that the latter type of bundle is never found in the cone. Now, it is a well known and widely accepted generalisation, that reproductive are more conservative than vegetative axes. Further, bundles with continuous xylem are characteristic of the primary internodal axis of *E. maximum*, the only one with which we are acquainted except that of *E. variegatum*, the bifascicular stele of which is clearly reduced. Again, though from the phylogenetic point of view a knowledge of the internal structure of the Mesozoic Equisetales is much to be desired, we possess numerous descriptions of the axes of the palæozoic Equisetales, the Calamariæ, and, in no case, so far as I am aware, is there any evidence for the existence of bundles with three groups of xylem.

It is suggested, then, that the type of bundle which is usually regarded as the typical internodal form has arisen in the phylogeny from a bundle in which the xylem was continuous, owing to the failure of some of the cells of the metaxylem to develop as tracheides. It would seem that in most cases, at least, the mass of xylem had become U-shaped before its fragmentation. It is quite probable, however, to judge from the varied position of the lateral metaxylem groups (these may be divergent, parallel or even convergent) and from the differences in their outline, that the persistent tracheides have, in some cases, undergone a certain shifting in position since their separation from the protoxylem. Usually, apparently, the cells which ceased to develop as tracheides seem to have been those near the carinal group, *i.e.*, those at the bend of the U. But Quéva has pointed out that when in the rhizome of *E. maximum* or *E. limosum* a lateral metaxylem-group is reduced to a single tracheide, this is often in contact with the carinal canal (14, p. 30). Here, then, the cells which fail to develop as tracheides are the outer elements of the metaxylem. I have noticed that in *E. giganteum*, in the part of the axis between the annulus and last whorl of leaves, in which, as already noted, lateral metaxylem may be wanting or much reduced, a single large tracheide not infrequently represents the only metaxylem present, and that it may abut on the carinal canal, or be situated at the periphery of the bundle. In fact, while reduction of the xylem of the bundle seems generally to

have been caused by the obsolescence of the elements of the metaxylem abutting on the protoxylem-group, any of the elements of the metaxylem may cease to develop as tracheides. This is only what we should expect in view of the fact that sometimes there is no lateral metaxylem.

If we accept the view that the lateral groups of metaxylem are parts separated from the protoxylem relatively recently in the phylogeny, the question as to whether these lateral groups contribute to the formation of the trace seems of less importance. It is possible to reconcile the late Mr. Gwynne-Vaughan's denial of the existence of this contribution (9) with Mr. Eames' assertion of such a contribution (7, p. 593) by supposing that the metaxylem may contribute to the trace if the latter is unusually large or the carinal group of protoxylem relatively less well-developed, while in other cases the carinal group of tracheides may itself suffice for the emission of traces.

We have not so far discussed the vexed question of the direction of lignification of the lateral groups of metaxylem. The fact that, more often than is usually believed to be the case, they are not separate from the carinal canal is not, of course, incompatible with their centripetal development. Still, very possibly, but for their supposed independence from the protoxylem, the late Mr. Gwynne-Vaughan might never have asserted their probable homology with centripetal xylem. This author did not mention, possibly he overlooked, an earlier assertion than his of the centripetal development of the lateral strands of wood. Poirault, in a paper read as early as 1887, and published in 1890, stated that the lateral xylem of the bundle of *Equisetum* developed centripetally (14, p. 13). It is true that he called this lateral wood "secondaire"—a misleading expression, for to judge from his description he does not regard the lateral tracheides as being formed by a cambium, but merely uses the word "secondaire" to bring out the contrast between the metaxylem and the protoxylem, the elements of which he describes as "primary vessels." Since the first publication of Mr. Gwynne-Vaughan's views, however, have appeared Quéva's excellent figures of developmental stages of the metaxylem. The latter's very careful descriptions, based on material giving remarkably complete series of stages, seem to show that the lateral metaxylem develops centrifugally (15), though probably, as pointed out by Mr. Eames (8, p. 592), there is some irregularity in development.

The nature of the ring of short reticulate tracheides known as the nodal, or more accurately the supra-nodal xylem, is one which

can only be very briefly touched upon here. After Quéva's researches there seems every reason to regard it as primary (15, p. 21). In that case it may represent a fresh development of wood, or, as seems to me more likely, it may be a modification of the ordinary primary centrifugal xylem of the axis. But whether it be regarded as a modification or a fresh development, it is difficult not to connect its retention during reduction of vascular tissues, or its development, with the presence of numerous appendages at the node. In such British species as I have examined, and in the small cone-bearing branches of *E. giganteum*, I have never seen any indication of the separate existence of the lateral strands inside and over the ring of reticulate nodal tracheides, which Mr. Gwynne-Vaughan claims to have observed in the nodes of *E. giganteum*. But such persistence of the lateral bands would not be incompatible with the phylogenetic unity of the Equisetaceous bundle. The fact that such a large number of appendages requiring vascular supply are initiated, even though they are not always fully developed, at most of the nodes of the vegetative axis of *Equisetum*, in spite of the relatively poor development of xylem in the internodes of these axes, has hardly received the attention that it deserves.[1] As regards the usual position of the lateral metaxylem of the internode it may be pointed out that the vascular supply of the branches is inserted on the ring of xylem vertically above the point at which two adjacent groups of metaxylem, each belonging to a different bundle, have fused. It seems not unlikely that the position of the persistent metaxylem at the sides of the bundle is correlated with the need for emission of a vascular supply to the branches, each of which lies midway between two leaf-traces. In this connection it is significant that the tendency of the lateral metaxylem to reduction—a tendency sometimes leading to complete abortion—is relatively pronounced in the rhizome, where comparatively few branches develop. Again, in *E. limosum* and sometimes in *E. giganteum*, the internode below the annulus seems to contain little or no metaxylem. It is possible that this observation should be brought into relation with the fact that at the reduced node of which the annulus marks the position (Browne, 2 and 3), no lateral branches are normally developed or even initiated. In other words, if, as seems to be established, the annulus is a reduced leaf-sheath, the reduced node at which it is inserted probably lost the capacity to

[1] The frequent presence, in unbranched or poorly branched axes, of numerous dormant branches, provided with a fully developed vascular supply, seems to show that reduction, or loss, of branching is a recent character in the phylogeny of the genus.

initiate branches relatively early in the phylogeny; and correlated with this loss certain species have ceased, or are ceasing, to produce lateral metaxylem in this region.

Perhaps, even to-day, it is not useless to add that in expressing the conviction that the internodal strands of *Equisetum* are phylogenetic units that may conveniently be termed bundles, it is by no means intended to suggest that these strands are in any strict, scientific sense equivalent to the ordinary internodal bundles of the Angiosperms. The fact that such bundles are common, whereas, in *Equisetum*, the bundles contain some purely cauline vascular elements, constitutes a real difference between the two types. Moreover, it seems particularly gratuitous to seek for strict stelar homologies between groups so remote from one another and of such very different antiquity as the Equisetales and the Angiosperms.

LITERATURE QUOTED.

1. Bower, F. O. "The Origin of a Land Flora," 1908.
2. Browne, I. M. P. "Contributions to our knowledge of the Anatomy of the Cone and Fertile Stem of *Equisetum*." Annals of Botany, July, 1912.
3. ,, ,, "A Second Contribution to our knowledge of the Cone and Fertile Stem of *Equisetum*." Annals of Botany, April, 1915.
4. Buchtien, O. "Entwicklungsgeschichte des Prothalliums von *Equisetum*." Bibliotheca Botanica, No. 8, 1887.
5. Campbell, D. H. "Mosses and Ferns." Second edition, 1905.
6. Duval-Jouve, J. "Historie naturelle des *Equisetum* de France," Paris, 1864.
7. Eames, A. J. "On the Occurrence of Centripetal Xylem in *Equisetum*." Annals of Botany, October, 1909.
8. Fritel, P. H. and Viguier, R. "Les *Equisetum* fossiles et leur structure." Revue générale de Botanique, 1909.
9. Gwynne-Vaughan, D. T. "Remarks upon the Nature of the Stele of *Equisetum*." Annals of Botany, 1901.
10. Kidston, R. E. "On the Fossil Flora of the Staffordshire Coal Fields, Part III. The Fossil Flora of the Westphalian Series of the South Staffordshire Coal Field." Transactions of the Royal Society of Edinburgh, Vol. L., Part I, No. 5, 1913-14.
11. Leclerc du Sablon. "Sur les tubercules des Equisétacees." Revue générale de Botanique, 1892.
12. Milde, J. C. "Monographia Equisetorum." Nova Acta Academiæ Leopoldino-Carolinæ, XXXV, 1867.
13. Poirault, G. "Recherches d' Histogénie Végétale." Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg." 7th Séries, Vol. 37, No. 11, 1890.
14. Quéva, P. "Histogenèse et Structure de la Stipe et Fronde d'*Equisetum*" Mémoires de la société d'histoire naturelle d'Autun, 204-411, 1907.
15. Ramey, E. "Sur quelques espèces tuberculeuses du genre *Equisetum*." Mémoires de la Société des Sciences physiques et Naturelles de Bordeaux, 1855.

MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER I.

Introduction.

THE adoption of experimental methods of evolutionary study early in the present century was accompanied by sanguine hopes that a general and universally applicable method of evolution might thus be discovered. But two decades of intensive experimental work with plants and animals has led to a greater diversity of opinion concerning evolutionary factors than ever before. Wherever a particular species or group of forms has been intensively studied, the results have illuminated a particular field of inquiry concerning evolution. But other results, dealing with organisms having different bionomic relations, have answered other questions and at the same time propounded new series of problems. While there has therefore been a great accumulation of data concerning the variations of organisms, the inheritance of characters new and old, and the relations and reactions of these organisms to their varied environments; yet this has led to no unitary result which can be universally applied. These experiments have rather served to emphasize the manifold character of the evolutionary process.

Not only have various groups of organisms contributed their quota to this multifarious result, but different methods of experiment and different fields of observation have no less clearly tended to emphasize particular evolutionary factors. Individual bias has also of course played a part in the interpretation of many results.

Important and valuable as these experimental studies have been in opening a new era of evolutionary investigation, and leading to very definite conceptions concerning heredity and many aspects of variation and distribution, yet I believe they have been perhaps most generally useful in a direction which has not as yet been recognized. For their very variety, apart from interpretations put upon them, is sufficient to show that in the search for one all-explanatory evolutionary principle, man is following an *ignis fatuus*. Darwin recognized this even in his day, for while he laid chief stress upon natural selection, he also relied upon the Lamarckian factor,

and to some extent on the direct effect of environment. But Darwin's followers at the end of the nineteenth century, having eliminated other factors, were endeavouring to show that natural selection was sufficient to account for all the then known phenomena of variation and adaptation. In the meantime palæontologists and anatomists, particularly the American School of Neo-Lamarckians, had kept alive the Lamarckian factor. Following that period, the striking discoveries in connection with mutations and Mendelian inheritance opened up a new outlook.

Darwin made no clear distinction between continuity and discontinuity in variation or inheritance, although his language sometimes clearly implies that he had observed one thing or the other. In some cases infinitesimal variations were apparently in his mind in writing, but when he refers to "individual differences" it is usually clear that he is citing what we should now call small or parvigrade (Poulton) mutations. In one aspect then, mutation as an evolutionary factor represents a refinement and an increased precision in the application of Darwin's theory of natural selection. That he recognized the occurrence of variations which were not necessarily subject to natural selection is clear from such passages as the following in the "Origin": "I am inclined to suspect that we see, at least in some of these polymorphic genera (such as *Rubus*, *Rosa*, *Hieracium* and fossil Brachiopods), variations which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection" (p. 33).

If we go but a step further, and assume that these variations are followed by others in the same population with elimination of some steps by selection; or if we assume the immediate origin of new specific types through single mutations, and their gradual spread from the centre of origin, then we are using the mutation theory of de Vries as it is widely applied at the present time. Darwin's objections to "sudden and considerable deviations of structure" as material for evolution, were based largely upon his observations of wide saltations and monstrosities. They included the well-known argument of swamping through crossing, which has since been negatived by the Mendelian discoveries.

It cannot then be said that the present Mendelian-mutationist attitude in its general aspects represents more than a refinement of Darwin's main thesis, based upon greatly increased knowledge of variation, inheritance, and cell structure; and a restriction of

the incidence of natural selection. Nevertheless this increased precision is of vast importance, because it is based upon a multitude of actual breeding experiments and accurate observations.

But while mutationist conceptions have been coming in as a refinement of Darwinism, other elements of the problem have not been left without attention. Much has been written concerning isolation, the adaptation of geographic races, and orthogenesis; while even crossing has been raised by some to the importance of an evolutionary factor. While these pages are primarily a discussion of mutation as an evolutionary factor, an incidental consideration of some of the other factors will be necessary, in order to give mutation its proper setting in the picture.

As mentioned above it appears probable that the era of the vain search for a single evolutionary principle is now at an end. That end has been chiefly brought about by the experimental researches in genetics on the one hand and the work of animal palæontologists on the other. While palæobotanists have been actively accumulating valuable historical data, it does not appear that palæobotany has yet much direct evidence to offer concerning the causes or methods of evolution in plants. The reason for this probably lies in the greater difficulties of method involved in palæobotanical research. The animal palæontologist may be able to determine or identify an animal from the mere outline of a single bone or a few portions of the skeleton. The fossil botanist must rely largely upon sections of material which is so preserved as to show the details of histological structure.

All the known evolutionary factors have in turn had their advocates, who usually attempted to make their application universal. We have had the Lamarckian factor of use and disuse, natural selection, isolation, direct adaptation ("epharmosis"), orthogenesis, mutation, the unpacking of Mendelian factors, and crossing, as explanatory principles. Their failure in universality has been apparent enough in every case. On the other hand, many of these factors and perhaps all, may be reasonably claimed to have had some share in the evolutionary result. Each advocate may be expected to press his claim as far as possible, but there are obvious limiting factors with regard to every one of these principles the moment we begin to examine them; and it is only by limiting the field of vision or deliberately closing our eyes to other facts, that a belief in the universal application of any one of them can be retained.

Any future evolutionary principle which aspires to universality must consist in a synthesis or integration of these factors, or such of them as can be proved to be sound in the fields of their application. The time for unlimited advocacy of single exclusive factors is past. Future advance in the understanding of evolution must then consist in the determination of the limitations of each factor, and the weaving together of such elements as are sound, into a connected whole.

The recent attempt of Osborn (1918) to deal with organic evolution from the energy standpoint, while not as yet markedly successful, may perhaps represent a line of approach through which a synthesis of evolutionary factors, may ultimately be reached. Whitman's (1919) elaborate studies of evolution in pigeons are grounded upon energy conceptions. The great accumulation of palæontological material which has taken place in recent years, gives vertebrate palæontologists a solid substratum of fact on which to construct hypotheses, which experimentalists can no longer afford to ignore. Gaps in mammalian phylogenies, for example, have been filled up to a remarkable extent, so that many of the older arguments drawn from the imperfection of the geological record are no longer applicable. The wonder is rather at the completeness, variety, and abundance of the skeletons preserved in deposits and unearthed by man.

A re-reading of the *Origin of Species*—an exercise which any biologist could profitably indulge in, at least once in every five years—serves on the one hand to emphasize the greatness of Darwin's vision, and on the other to encourage the present scientific man by showing the immense accumulation of accurate knowledge concerning organisms which has taken place since Darwin's time. The problem of to-day, just as it was in 1859, is to bring all these facts to bear upon the explanation of the diversity of organic species. In connection with this task not one of the modern biological sciences can be safely ignored, and such physical sciences as astronomy, geo-morphology, physiography, chemistry and many aspects of physics must be pressed into service. Darwin dealt with variation in wild and domesticated animals and plants; heredity; the relations of organisms to each other and to their inorganic environment, hybridization and sterility; the geological record; geographical distribution; and embryology; in so far as the knowledge of his time permitted. In every one of these fields, except perhaps the broader principles of plant distribution, the

subsequent advances have been enormous. Many new sciences, such as cytology, bio-chemistry and ecology, have come into existence, and have made possible an insight into organic structure, constitution and relationship which was undreamed of even half a century ago.

Just as it is rash to attempt to interpret heredity and variation without a knowledge of the microscopic details of cell and nuclear structure or the physiology of hormones, chalones and enzymes; so it is equally unsafe to explain many questions of distribution without an intimate knowledge of the ecology and physiology of the organisms concerned. The burden of knowledge laid upon the modern evolutionist is thus so great that no one measures up to the possibilities, and it becomes necessary for the worker in one field to obtain second-hand his knowledge of the results in other fields. But it is none the less incumbent upon him to utilize these results intelligently if evolutionary science is to advance.

This is particularly true of such disciplines as the experimental study of heredity and the investigation of cell and nuclear structure, which had their historical origin in complete independence of each other and have since converged so closely that their results are mutually interwoven. Rarely in the history of science has such a remarkable convergence taken place. Modern genetics represents a synthesis of these two sciences into one. Many genera of plants and animals have now been attacked from both aspects, that of breeding experiments and that of cell structure, with mutually beneficial results; and it is too obvious to need pointing out that the present position of genetics, both in our knowledge of heredity and of variation, could not possibly have been attained without such combined studies. *Œnothera* and *Drosophila* are conspicuous examples but there are many others in the recent literature. In future these two sciences cannot afford to stand alone, but must derive mutual support from each other. Interpretations of breeding results, especially those introducing new complications, which ignore or run counter to well known cytological facts, will have little chance of acceptance. Cytology in its turn will greatly benefit by more comparative studies of related races and species, such as are now being made in a number of plant and animal forms. In such way it is to be expected that a synthetic understanding of genetic phenomena from the combined structural and functional or physiological aspects may be attained.

CHAPTER II.

Foundations of the Mutation Concept.

In later chapters we shall deal with the occurrence of mutations in a wide range of wild plants and animals. The writer's book on mutation[1], dealt particularly with the mutations of *Œnothera* and the conclusions to be drawn from them. A cell theory of mutations was formulated, based on the cytological and breeding work with *Œnothera* and incidently a wide range of other forms; and concepts were developed which proved applicable to many other plants and animals. This has involved certain departures from the theory of mutations as originally propounded by de Vries. Instead of the purely hypothetical and conceptual pangens, whose alterations were the putative cause of mutations, it has been possible to link up many of the changes in *Œnothera* with visible structural changes in the chromatin of the cell.

Let us consider for a moment the simplest case of this kind. It is already well-known, but requires restatement because some writers have endeavoured to deny the significance of the facts. The *lata* mutation is now known to occur in *Œ. lamarckiana*, *Œ. biennis* and *Œ. suaveolens.* The peculiarities are the same in every case—obtuse-tipped, deeply crinkled leaves, a somewhat weak or irregular habit of growth, stout rounded buds, almost completely sterile anthers, and 15 chromosomes in the nuclei. This constellation of characters is super-imposed on, or rather substituted for, the characters of the species in each case, and the same mutation has also been observed from some of the mutants of *Œ. lamarckiana* and also in various hybrids. Thus *Œ. biennis* mut. *lata* has small flowers while *Œ. lamarckiana* mut. *lata* has large flowers, but the *lata* forms otherwise agree. *Œ. lata rubricalyx*, two of which occurred in the F_2 of *rubricalyx* × *grandiflora* had *lata* peculiarities combined with the red pigmentation of *rubricalyx*.[2] It is also significant that *lata* mutants sometimes occur in pairs.

Only one hypothesis based on observation has been suggested to account for the origin of *lata* with its 15 chromosomes. In 1908 occasional irregular reduction divisions in the pollen mother cells were observed in *Œ.* mut. *rubrinervis* whereby an 8-6 separation of chromosomes took place in the heterotypic mitosis. This would lead to the formation of two pollen grains with 8

[1] Gates, 1915. [2] Gates, 1914; Gates and Thomas, 1914.

chromosomes and two with only 6. The same irregularity has since been seen in various other types. There can be no reasonable doubt that *lata* originates in this way, through the union of a germ cell having 8 with one having 7 chromosomes, unless we deny some of the best established facts in cytology. Stomps, however (1916), goes so far as to deny the probability of this hypothesis, although he does not venture to offer anything in its place. His denial is based on the fact that several mutant types are known to have 15 chromosomes. But, as has been pointed out,[1] if the 7 gametophyte chromosomes are unlike, as is probable from many general cytological considerations, then 7 distinct types with 15 chromosomes are to be anticipated. Up to the present, no such number of forms having 15 chromosomes has been described from any strain of *Œnothera*, nor have seven such forms been authenticated altogether, although there is no obvious reason why they should not ultimately be found.

The evidence, then, is clear and definite that *lata* originated through a chromosome entering the wrong nucleus in the reduction division. In this way two pollen grains, or one megaspore will be produced, each having 8 chromosomes in its nucleus. The presence of the extra chromosome, as a duplicate of one, will no doubt immediately have its effect on the cytoplasm of the pollen grain or megaspore containing it. So that the mutation must quickly become a property of the cell as a whole, and, theoretically, at least, this will alter the character of the whole male or female gametophyte derived from a spore with 8 chromosomes, though the differences may not always be demonstrable by the microscope. Renner (1919) has shown that visible differences exist between the pollen grains and male gametophytes of various species, and that segregation of these characters takes place in the pollen of the F_1 hybrids. If an egg from a mutated megaspore has 8 chromosomes, it is already different both in nucleus and cytoplasm from an ordinary egg of the type, since the extra chromosome has been producing its effect thoughout all stages of the embryo-sac formation. Nevertheless, the only original change which it is necessary to assume, to account for the appearance of *lata*, is a chance irregularity in which both members of a pair of chromosomes enter the same nucleus in the reduction division. To endeavour to explain the origin of *Œ. lata* through an alteration in a hypothetical pangen when the visible facts of the chromosome structure are so clear, is to desert science for obscurantism.

[1] Gates, 1915, p. 181.

The same irregularity has been observed in animal spermatogenesis and found to produce individuals with one or more extra chromosomes, *e.g.*, in *Metapodius* (Wilson 1909), where the Y chromosome may be represented as many as 6 times in the cells of certain individuals. The most striking case in animals is known as non-disjunction in *Drosophila melanogaster*, where it has been studied by Bridges (1916) in great detail. This consists in duplication of the X or Y chromosomes through both passing to one cell in spermatogenesis, and it leads to the production of individuals whose heredity behaviour, as in *Œ. lata*, is peculiar owing to the presence of these extra chromosomes. It also results in the formation of certain non-viable and sterile types. The whole situation, though very intricate, is perfectly clear, and the chromosome behaviour corresponds with that previously described in *Œ. lata*. Any sceptic cannot do better than study conscientiously this excellent paper of Bridges. No one who studies this subject with any attempt at an impartial frame of mind can fail to agree that the chromosome content of the various individuals determines the differences in their hereditary behaviour. Indeed, it is not too much to say that most of the arguments against a chromosome basis of heredity are based on sheer unfamiliarity with the enormous advances in this subject which have taken place in recent years.

It must not be inferred from the preceding remark that the whole mystery of heredity is believed to have been solved. Such a conclusion would be contrary to the history of every branch of science. It is recognized that no "explanation" is final, but that each discovery represents a further step in analysis, whether it be in the processes of inheritance or in the structure of an atom. The evidence for the independent identity of chromosomes is at the very least equal to that for the existence of electrons, emanations and other particles constituting the atom. Fortunately, physicists are not worried by the argument that until the exact nature of electrons and corpuscles is known it is unsafe to recognize their existence in formulating a hypothesis of atomic structure. But this is the type of argument with which the cytologist is frequently confronted, coming from biologists whose knowledge often does not extend to the chromosomes. The chromosomes are structural facts whose existence can no longer be ignored in any fundamental analysis or interpretation of the structure, development, inheritance or other properties of organisms.

Just as the cell theory of organic structure has long since passed into the realm of fact, so in a sense has the chromosome theory of inheritance. We need mention only three of the most striking cases where a definite relationship has been established between a particular chromosome complex and a certain set of external characters. These are (*a*) the sex chromosomes, now known to show dimorphism in a wide range of animals, and recently discovered in a liverwort (Allen 1919); (*b*) the aberrant chromosome conditions in the *Œnothera lata* series of forms; and (*c*) the non-disjunction phenomena in *Drosophila.* In all these cases, without obscuring the issues by introducing the concept of "causality," it is definitely known that a certain set of external features of the organism is associated with a certain structural complex of its nuclei, and this complex has been passed on by mitotic division from its inception in the fertilized egg. This is not hypothesis but fact. *Œnothera lata* whenever it is examined (some 50 individuals have had their chromosomes counted) invariably shows the extra chromosome in its mitotic figures. The spermatocytes or the embryonic tissue of the males in various groups of insects show the characteristic male constellation of chromosomes, *i.e.*, with an X or an XY group in addition to the autosomes, while the females show a corresponding XX group.

While we must therefore regard the "chromosome theory," like the cell theory, as an established fact up to a certain point, so, again like the cell theory, must we also regard it as subject to qualifications and limitations.

Since we are not here discussing the general arguments for a more minute and detailed relationship between the chromatin and the complex of inherited characters, this aspect of the subject may be left for the present, with the remark that in the three classes of cases cited a definite relationship which may be classed as hereditary has been clearly established between particular external features and particular chromosome complexes of the nuclei.

(To be continued).

CAMPYLONEMA LAHORENSE, A NEW MEMBER OF SCYTONEMACEÆ.

By S. L. Ghose, M.Sc.

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[With Six Figures in the Text.]

In Lahore in the month of August during the rains, a very beautiful blue-green alga makes its appearance on lawns and waste grounds where water stands for a day or two and then slowly dries up. In damp places thus left after the evaporation of water, small, shiny, bluish-green, circular patches are seen amongst tufts of grass. These slowly extend on all sides and become irregular in outline till finally they run into one another and produce a very wide, woolly, bright bluish-green stratum on the surface of the damp soil. As the soil dries the stratum takes on a brownish tinge till finally when it is quite dry it becomes dark-brown. A healthily growing vegetative stratum is partly embedded in the mud and is partly above it (Fig. 1). In the subterranean part the filaments

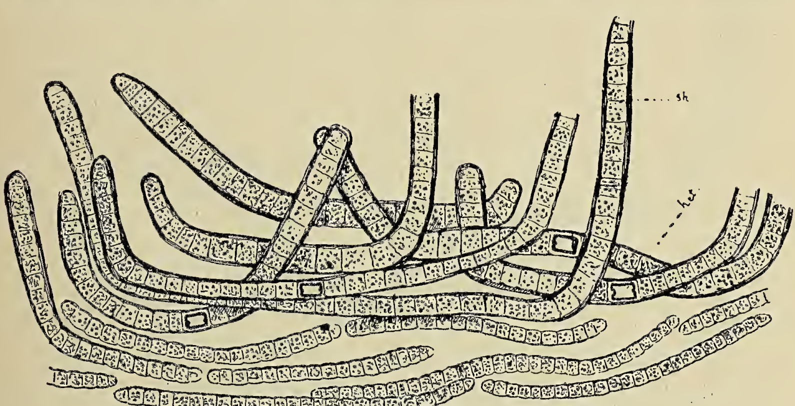

Fig. 1. A small portion of the thallus, showing the filaments in its embedded and aerial portions. *sh* sheath, *het* heterocyst × 286.

are straight, of lighter colour, run more or less parallel to one another and have no distinct sheaths. Those near the surface of the soil are generally curved in the middle and have the two ends abruptly ascending into vertical aerial arms. Each of these exposed arms is enclosed in a sheath, which is thin and hyaline at first, but which later on becomes thick and lamellose, and brown or yellowish-brown in colour (Fig. 2). As the soil dries the sheaths extend towards the middle of the filament and might finally meet so as to enclose the whole of it.

The filament. The filaments measure up to one and a quarter m.m. in length, the matureones being curved in a more or less semi-circular manner. Occasionally pseudo-branches are given off, either singly at the base of an heterocyst (Fig. 3) as in *Tolypothrix*, or rarely in pairs—generally in old filaments—between two heterocysts (Fig. 4) as in *Scytonema*. Trichomes 6-9μ thick, bluish-green, slightly constricted at the joints. Cells 5·11μ long, with coarsely granular contents. Dissepiments are generally not very distinct in mature filaments, but are easily seen in hormogones or young filaments.

The sheath. The sheath is at first thin and hyaline, but later on becomes thick, often lamellose and yellowish-brown, up to one micromillimeter thick. It is very inconspicuous in filaments or portions of filaments embedded in mud, but in exposed filaments or parts of filaments it is brown, firm, thick and tightly adhering.

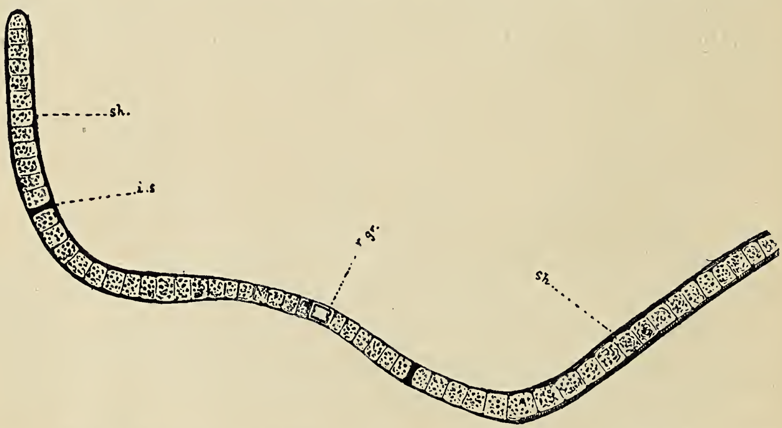

Fig. 2. A typical filament showing the incomplete sheath, median heterocyst, and inter-cellular substance. (*i.s.*) *r.g.* refractive granules × 286.

Heterocysts. One heterocyst is, as a rule, found in the middle of the filament (Fig. 2). Sometimes, however, two heterocysts are found side by side at this place (Fig. 5). Other heterocysts are situated at intervals through the whole length of the filament (Fig. 3). The heterocysts are at first pale yellow in colour and have some finely granular contents. Later on they lose these contents and become hyaline. The refractive granules situated adjacent to the pores at each pole, as mentioned by West (4) and Fritsch (1), are quite easily seen in most cases (Fig. 2). The heterocysts are $12\text{-}21\mu$ long, $7\text{-}9\mu$ broad, and rectangular or ellipsoid in shape.

Perennation and Multiplication. In unfavourable conditions such as drought, as a rule, the filaments lie enclosed in their thick sheaths, thus giving the stratum a dark-brown colour. They are very fragile in this condition. When the favourable conditions recur, trichomes, generally broken up into a number of hormogones, slowly come out of the sheaths and lie more or less parallel to one another, thus forming a fresh bluish-green stratum. These hormogones may consist of even one or two cells. They resemble the filaments of *Oscillatoria* in general appearance and may be easily mistaken for the latter. They are produced generally by the secretion of an inter-cellular substance or sometimes by the death of vegetative cells here and there. The inter-cellular substance is dark-green in colour and is in the form of a biconcave disc (Fig. 2).

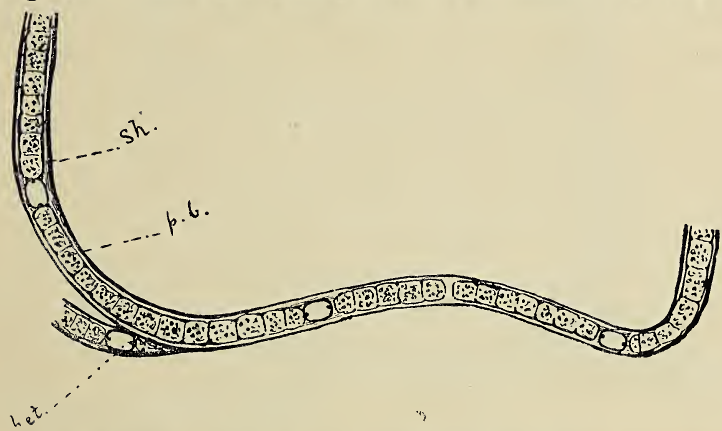

Fig. 3. A filament showing many heterocysts *(het.)*, and a single pseudo-branch *(p.b.)*, at the base of one of them. (× 450).

Rarely spores were seen forming a chain inside the sheath. The sheath in these cases was found to be thin and smooth, though firm and brown (Fig. 6). Each spore has a thick smooth outer membrane and a very thin inner membrane. It is about 8μ long and about 6μ broad and has homogeneous or very finely granular contents. The ejection and germination of these spores have not yet been seen by the writer.

Systematic. The alga described above, although to some extent it resembles *Tolypothrix arenophila* W. and G. S. West, and was to that species by the writer in a former paper (2), shows many characters which render it hardly possible of reference even to the genus *Tolypothrix*. Firstly, heterocysts are frequently found at intervals during the whole length of the filament as in *Scytonema*, and are seldom confined to the base of a

pseudo-branch as in *Tolypothrix.* Secondly pseudo-branches themselves are very rare, and as a rule, filaments are unbranched, though having one or more heterocysts. Even when pseudo-branches are present they are given off singly or in pairs as has been mentioned above, thus partaking of the characters of both *Tolypothrix* and *Scytonema.* A third characteristic is the curved shape of the filament.

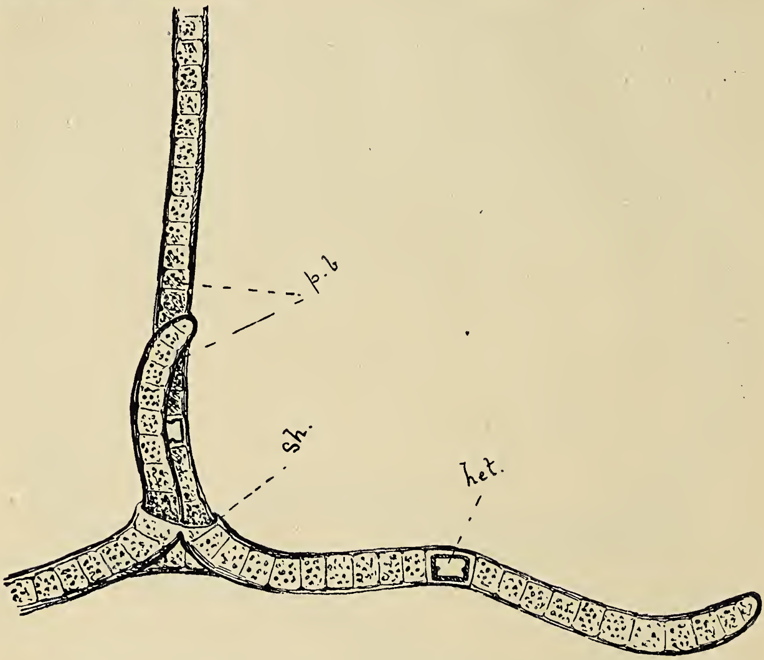

Fig. 4. An old filament showing the thick sheath and paired pseudo-branches. (× 450).

The genus *Campylonema* was monographed by Schmidle in 1900 (3) to include members of the Scytonemaceæ with generic characters resembling those of the alga described above, with the exception that no mention of the presence of spores was made. Only one species, *C. indicum* Schm. has been described from Bombay, from which the alga under discussion differs in many respects. It is not epiphytic on Hepaticæ like *C. indicum*, but occurs on damp soil forming a vast stratum. The thallus is thin and woolly and not fasciculate and crisp as in *C. indicum.* Trichomes are not very torulose and ramose upwards as those of *C. indicum*, and are not so thick as the latter.

For the above reasons I propose to refer the alga described in this paper to the genus *Campylonema* and to create a new species,

Campylonema Lahorense with the following specific characters:—Thallus woolly, bright bluish-green or bluish-brown, terrestrial, partly embedded in mud and partly above it; sheath inconspicuous, thin and hyaline in the embedded portion, and firm, thick, lamellose, tightly adhering, and brown in the exposed portion; filaments curved in a more or less semi-circular manner, up to $1\frac{1}{4}$ mm. in length; trichomes bluish-green, 6-9μ in diameter, slightly constricted at the joints, rarely pseudo-branched, pseudo-branches given off singly or in pairs; cells isodiametric or a little longer or shorter than the diameter; transverse walls scarcely conspicuous in older filaments; heterocysts median or found at intervals

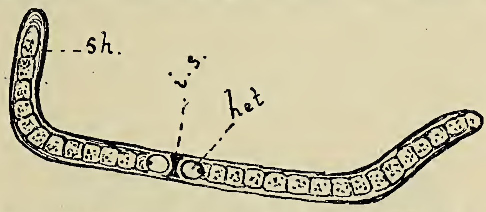

Fig. 5. A filament showing two median heterocysts. (× 400).

through the whole length of the filament, rectangular or ellipsoid, 12-21μ long and 7-9μ broad; spores 7-11μ long and 5-7μ wide, formed in a chain within the sheath, with brown thick and smooth episporium; cell-contents coarsely granular.

Habitat:—On damp lawns and waste grounds at Lahore, India.

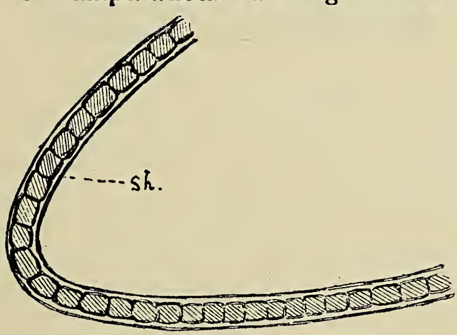

Fig. 6. A filament forming a chain of spores. (× 450).

REFERENCES TO LITERATURE.

1. Fritsch, F. E., ('04). Studies on Cyanophyceæ. New Phytologist, iii, No. 4, 1904.
2. Ghose, S. L., ('19). The Myxophyceæ of Lahore. Journal of Indian Botany, Vol. I, No. 1. 1919.
3. Schmidle, W., ('00). Hedwigia, Bd. XXXIX, p. 181, 1900.
4. West, G. S., ('10). Cambridge Botanical Handbooks, Vol. 1, p. 181.

THE OCCURRENCE OF ACTINOMYCES-LIKE ENDOTROPHIC MYCORHIZA.

By Jean Dufrenoy.

(*Assistant, Biological Station, Arcachon, France*).

[With Five Text Figs.].

I.—*Mycorhiza in Adenostyles albifrons.*

1. *Ecology.* Small well defined patches of *A. albifrons* occur in the Beech woods of the Pyrénées, near Barèges, at heights of about 3700 feet. The vertical shoots bear leaves, heavily rusted by *Uromyces cacaliæ* and much fed on by *Chrysomela gloriosa.* Long fleshy rhizomes run horizontally, giving long horizontal roots, rich in trichomes for most of their length. Both rhizomes and roots trail in the superficial layer of *undecayed,* fallen leaves, so that the plant is very easily uprooted.

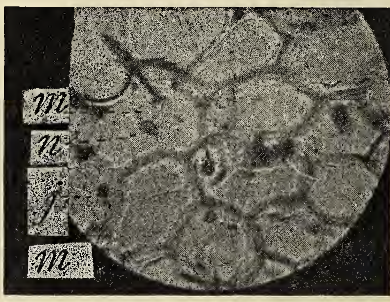

Fig. 1. Root of *Adenostyles albifrons,* transverse section, stained with carbolic crystal violet, then treated with I+KI. *m.* massue, gram positive. *n.* nucleus, within a net of hyphæ (not coloured) and their club-shaped "massues." *J.* nucleus of a non infected plamolysed cell. (Photomicr., oil imm. $\frac{1}{15}$ obj. Oc. 1., Stiassnie).

2. *The Endotroph.* Many hyphæ coil around the trichomes, and some of them push through the gelatinous pectic walls of the epidermal cells into the inner parenchymatous cells of the cortex, and even into the vascular system, the pericyclic tissues being heavily infected. Hyphæ show nearly as well in the cortex of the *rhizomes;* they were not observed in the petioles.

3. *Cytology of infection.* Roots were fixed in Bouin's picro-formol and hand-sectioned. Hyphæ were directly demonstrable by clearing with lactophenol, or staining with cotton-blue. But it is best to stain with carbolic crystal-violet, then to differentiate with amyl-alcohol, which stains the endotroph a deep blue, while the host-tissues display a light metachromatic rose-colour.

Hyphæ growing into some of the parenchymatous cells form a network round nucleus; locally they swell into little club-shaped masses ("massues"). These are either directly inserted on the hyphæ, or (as may occur in the rhizomes), terminate short lateral branches (Fig. 5, ct).

The hyphæ are acid fast and retain a red colour after coloration by carbol fuchsin and the Ziehl-Niellsen method. The "massues" are basophilous—and more so as they age; they are "gram positive," and stain a deep blue with cotton blue.

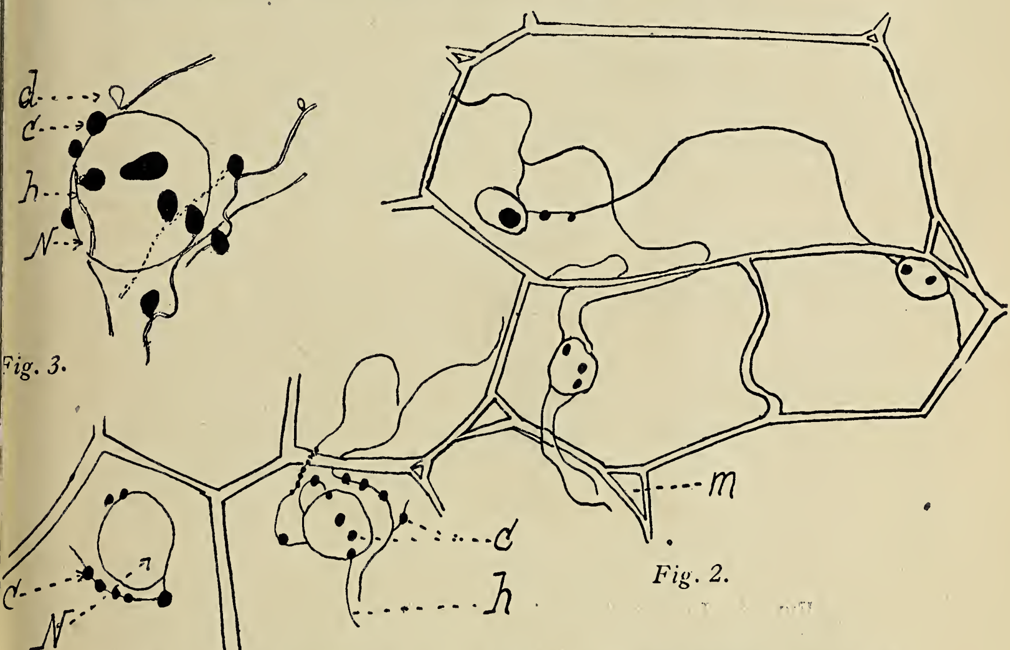

FIG. 2. From same section as FIG. 1. *N*. Hypertrophied nucleus of parenchymatous cell. *c*. club shaped "massues." *h*. hyphæ (uncoloured by alcohol).

FIG. 3. Nucleus of infected cell, showing detail of infection and relative dimensions of endotroph. (Oil imm. obj. $\frac{1}{15}$, oc. 9).
N. Nucleus, *c*, full grown "massues," (gram-positive) *d*, young "massue," *h*, hyphæ.

The nucleus in infected cells enlarges or may divide; the nucleolus becomes larger and basophilous. The whole of the nuclear material becomes granular and retains basic dyes, whereas the nuclei of the epidermal cells are acidophilous and stain deeply with eosine.

No hypertrophy of infected cells was observed, but hyperplasia may result from division by irregularly placed walls. Cytoplasm may shrink in neighbouring non-infected cells, which brings the nucleus into contact with the cell wall (Fig. 1).

II.—*The significance of "massues" in parasitic Actinomyces.*

Contrary to what we observe in the endotroph, the ordinary *Actinomyces* of "Actinomycosis" has acid-fast "massues" and basophilous hyphæ (1). Still we consider the club-shaped swellings in *Adenostyles albifrons* to have the significance of "massues" and therefore place this endotroph in the genus *Actinomyces*. Similar swelling-forming Endotroph has been reported by Peklo and Arzberger from the tubers of *Myrica gale*, and ascribed to an

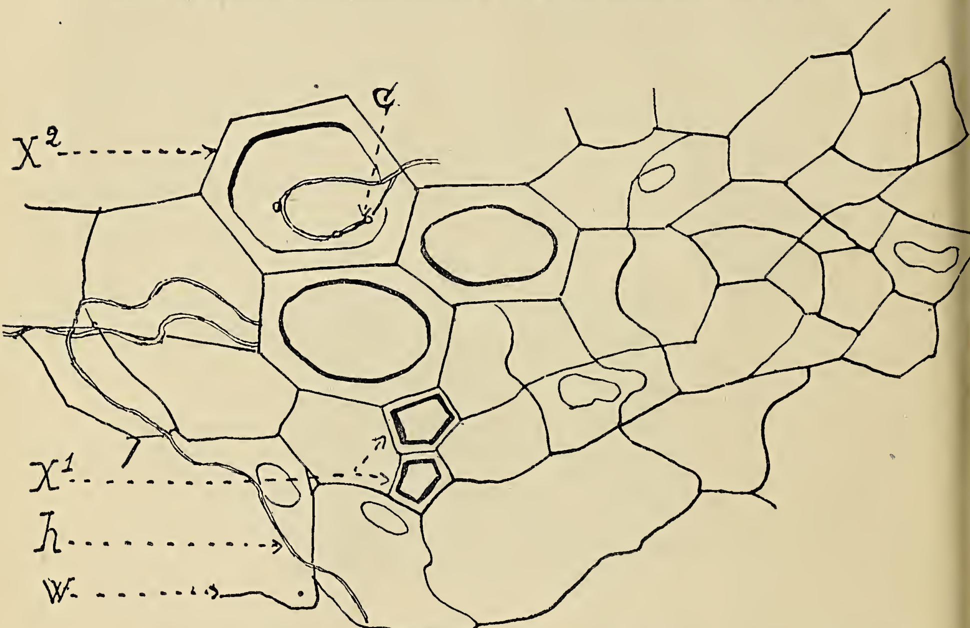

Fig. 4. Inner cortex and vascular tissues of root, coloured by the Ziehl-Nielssen method.

$X1$ protoxylem, $X2$ metaxylem, w, cell wall, h, hyphæ (about 2μ in diameter) c, "massues" (uncoloured by action of HNO_3).

Actinomyces, without any cytological evidence being adduced to enforce this conclusion (2). "Massues" indeed may be considered characteristic of *Actinomyces* growing in their infected hosts; they have also been recently reported from cultures submitted to the action of high temperatures or of various salts.

III.—*Conclusions.*

Actinomyces may be held responsible for two cases of endotrophic mycorhiza. This conclusion, however, being largely speculative, demands for further investigation of the cases and also a precise definition of the genus *Actinomyces* (3).

Infection *of the shoot* by endotrophs occurs in Compositæ as well as in Orchidaceæ and Ericaceæ (4, 5, 6).

FIG. 5. Rhizome of *A. albifrons*. Section of Cortex, coloured with Cotton blue (Oil imm. obj. $\frac{1}{15}$, oc. I). *ct.* terminal (acrogenous) "massue"; *N*, nucleus; *K*, granular nucleus; *h*, hyphæ.

LITERATURE.

1. Achalme. Actinomycose, in *Traité Hyg. Chantemesse*, 17, p. 1919, Paris, 1910.
2. Arzberger: *Ann. Mo. Bot. gard*, 1916, p. 87.
3. Drechsler, Ch. The genus Actinomyces, *Bot. Gaz.*, p. 65, Jan.-Feb., 1919.
4. Dufrenoy, Jean. NEW PHYTOLOGIST, 16, Oct.-Nov., 1917.
5. Péchoutre F. Rev., Bot. *Rev. Gen., Sc.*, p. 248, Apr. 1919.
6. Rayner, M.C. NEW PHYTOLOGIST, 15, Oct., 1916.

THERMAL LABORATORY, BARÈGES, 1919.

ELEMENTARY LECTURING WITH THE HELP OF SCHEDULES.

ELEMENTARY NOTES ON STRUCTURAL BOTANY, by A. H. CHURCH (12 lectures), Oxford Botanical Memoirs, No. 4., Oxford Univ. Press, 1919. Price 2s. net.

ELEMENTARY NOTES ON THE REPRODUCTION OF ANGIOSPERMS, by A. H. CHURCH (10 lectures), *Ibid*, No. 5., 1919. Price 2s. net.

THE method of teaching science by means of formal lectures followed by practical work in the laboratory, leaves much to be desired, especially in the case of elementary students. The fundamental criticism of this method from the standpoint of educational psychology is of course that the student is put into a passive and receptive instead of an active, critical, and executive frame of mind. He sits still and has information poured into him, and the active working of his own mind, without which real education is impossible, is apt to be at a minimum. And this unfortunate attitude, which is more or less forced on the student by the method of instruction in the lecture room, is only partially bettered by the cutting, inspection and drawing of sections which still forms the mainstay of the laboratory régime. Nevertheless the practical convenience of the method, especially to the teacher, is so great, that it still maintains itself in full vigour.

We are not concerned, at the moment, with suggesting alternatives, or with trying to determine the legitimate function of the lecture in teaching. But accepting the lecture system as an integral part of the method of instruction, it is clear that if the student takes his primary information solely or mainly from the lips of his lecturers, and records or tries to record what he hears in his notebook, he runs a grave risk both of failing to get his information accurate and of missing a large part of the real value of *vivâ voce* teaching. There's many a slip 'twixt the lecturer and the notebook, defective hearing, defective mechanism in the process of translating what is heard into what is written, slips in writing, and finally the failure to record what the lecturer says from lack of time. Any lecturer may convince himself that these failures of mechanism are very real by the simple process of inspecting his students' notebooks. As a method of communicating information the lecture is indeed largely a relic of mediævalism, of a time before the printing press made possible the accurate multiplication of copies of what a man has to impart.

All these considerations are of course the merest commonplaces to professional educationists, but they are very generally neglected by university teachers. Mr. Church, in his elementary teaching at Oxford, has adopted a method by which the defects of the ordinary lecture are largely overcome. The method is not new—the writer himself used it with success in one of the first elementary courses he ever gave, a great many years ago: it is to some extent embodied in all lecture courses of which a fairly full syllabus is issued; and for all we know it may be used extensively in the colleges and universities of the country. The method is simply to write down the substance of the lecture—the leading facts and ideas—in a condensed form, and to distribute copies, printed or otherwise multiplied, to the members of the class. Thus the student has, and knows that he has, the substance of what he would otherwise have to try to write down in his notebook, *in an accurate and authoritative form.* He is therefore free to *attend* to the lecture *with his whole mind*, being relieved from the strain of trying to get down as much as he can, and thus from the necessity of *attending*, not to what the lecturer is saying, but to what he said several seconds before. He can sit back and appreciate the lecture as a whole, get the whole thing into perspective, allow the light and shade, the varying emphasis, to make its full impression. Mr. Church expresses the difference by saying that whereas he used to lecture to a row of heads, with their attached hands writing for dear life, he now addresses a set of human beings listening to what he has to say. The only possible disadvantage of the method is that it enables the incorrigibly lazy student to be a little lazier, to leave his mind a blank or let it wander through the entire discourse. But it is doubtful if such students can be perceptibly benefited by any system of lecturing as such.

Secure in the knowledge that his class possesses copies of the main substance of his topic, the lecturer need not keep closely to the printed text. He may, if he chooses, elaborate special points, discuss further illustrations, develop side lines, or what not. He is no longer bound to plod laboriously through his basal data, for those are recorded in the leaflets. The printing press takes over the mechanical function of imparting cut and dried data, and both the lecturer and the class are free to enjoy the real irreplaceable advantages of *vivâ voce* teaching—the influence of the living personality of the teacher and the power of varying emphasis.

Each of Mr. Church's leaflets contains about 1400 words—as much as, or more than, a good elementary student could get down in his notebook in the course of an hour's lecture. Towards the end of the leaflet the material used in the practical work is introduced. The whole forms a condensed text-book representing twenty-two lectures, covering " two-thirds of the general elementary syllabus for the Preliminary Examination in Botany of the School of Natural Science " at Oxford, " a set on 'Lower Types' being required to complete the evolutionary scheme." We do not propose to criticise or comment on the actual contents of the leaflets, beyond making the remark that while doubtless no one will or should want to follow exactly the scheme of another teacher, these notes will be found intelligent, thorough and suggestive. We think Mr. Church has rendered a real service to university teachers by publishing his " Notes " and we commend them heartily to our readers.

One more point may be mentioned. There is a good deal to be said for issuing the notes of the entire course at the commencement, or, if the leaflets are issued separately, to give out each at the lecture before the one at which the corresponding topics are discussed. In this way the keener students can make themselves familiar with the skeleton of the lecture before it is delivered, and the lecturer can, in the case of small or moderate sized classes, ask questions on the substance of the schedule, and use the answers as a text for further explanation.

A. G. T.

JAMES WILLIAM HELENUS TRAIL, M.A., M.D., F.R.S., F.L.S.

JAMES W. H. TRAIL was born at Birsay, Orkney, in March, 1851. At the age of eleven, he was sent to school in Aberdeen, and some years later, on the appointment of his father to the Chair of Systematic Theology at Aberdeen University, that city became the permanent residence of the family, which thus returned to the region from which it had sprung.

The boy rather reluctantly went through the classical curriculum at school and college which was demanded by the tradition of his family and of his University alike. From an early

age his mind turned to natural history, and while a student he arranged and added to the collection of insects in the University Museum. His bent was not encouraged, but when he had completed his arts course, he was permitted to proceed to the study of medicine. Fired by the works of the early explorers of tropical South America, he hoped that an appointment as doctor to some expedition in that region would give him the opportunity of definitely adopting a scientific career. This hope was exceeded when in 1873 he went to Brazil as botanist to the Amazon Steam Navigation Company, and there spent two years in exploring the tributaries of the Amazon. In 1876 he accepted the post of botanist to the Colony of British Guiana, but in 1877, before he had sailed, he was appointed Regius Professor of Botany at Aberdeen University, succeeding George Dickie as the second occupant of the Chair. He was elected a Fellow of the Royal Society in 1893, and was President of Section K of the British Association in 1911. At his death after a short illness on the 18th of September, 1919, he was senior member of the Senatus of the University, with forty-two years' service.

Professor Trail's scientific work began with his papers on the Palms of Brazil in the *Journal of Botany* 1876-7, and was continued by a long series of contributions to the natural history of Scotland in the *Annals of Scottish Natural History*. In recent years he was most interested in the changes occurring in the native and introduced flora. He believed that these could best be traced and explained by the compilation and comparison of exact records of distribution, and devoted his energies to the task of amassing the necessary data. The material thus collected forms an invaluable record of the present distribution of the flowering plants, of the plant-galls, and of certain groups of fungi in Scotland. Carried to the finest point, his methods resulted in a study of the flora of the City Parish of Aberdeen, which will be published by the Aberdeen Natural History and Antiquarian Association. In it, the changes, mainly due to the influence of man, are minutely traced from the time of the earliest records. A collector of insects in his youth, he remained a keen entomologist with a wide knowledge of British forms. The galls formed a link between his two interests. All his work was permeated by the spirit of the early naturalists, which found its satisfaction in the observation of living things in the field.

The journey to South America coloured his whole outlook, and this was seen especially in his teaching. For illustrations of

the facts of biology and external morphology, on which he laid most stress in his lectures, he drew largely on his tropical experience. Many a doctor and teacher must look back on the Botany Class as a strenuous time. The lectures were held at 8 a.m., and evening and Saturday excursions were a prominent feature of the course. It was as necessary to be a good walker as a good observer, for the Professor's stride was long, and covered much ground in little time. The excursions were perhaps the most valuable part of his teaching; they permitted the free expression of his unequalled knowledge of plant life. A running commentary, to his immediate following, on the ways of plants and animals seen was interrupted only to name the plants brought to him. The reiterated warning that "scraps" were of no use was negatived by an unfailing identification of the most fragmentary specimen. His skill in "running down" plants of all classes was appreciated and made use of by a large circle of friends, acquaintances, and strangers; his help was extended to every applicant.

His students could always count on advice and assistance, and his kindly attitude has encouraged many to become scientists. Most have followed the lines he himself favoured and are occupied in systematic and economic work in our tropical dependencies and our museums. But his support was extended with equal warmth to those whose interests lay in other fields. Assistance took a generous and very practical form in the foundation of several University endowments.

Besides occupying the Chair of Botany he was Lecturer in Agricultural Botany to the North of Scotland Agricultural College, and his administrative activities were very numerous.

Professor Bower has termed him a "typical Aberdonian." Perhaps in that county the quality emphasised in Charles Darwin's motto is even more highly developed than in Britain as a whole. In the early tenacity with which he pursued his intention of being a scientist, no less than in the persistence with which he later carried on his investigations, Professor Trail showed that he too believed "It's dogged does it."

M. S.

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The objects of *THE JOURNAL OF ECOLOGY* are (1) to foster and promote in all ways the study of Ecology in the British Isles, serving as the organ of the BRITISH ECOLOGICAL SOCIETY; (2) to present a record of and commentary upon the progress of Ecology throughout the world. Its contents include original articles and notes on ecological topics of current importance, including methods of ecological study and research; notes on current work in the British Isles; reviews and notices of publications of general ecological bearing, of work upon British vegetation, and of work upon foreign vegetation; general correspondence; reports and notices of meetings of the British Ecological Society; progress of the Nature Protection movement and of ecological work in Nature Reserves.

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Editorial communications to A. G. Tansley, Grantchester, Cambridge

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EDITED BY A. G. TANSLEY, M.A., F.R.S.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

IN CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

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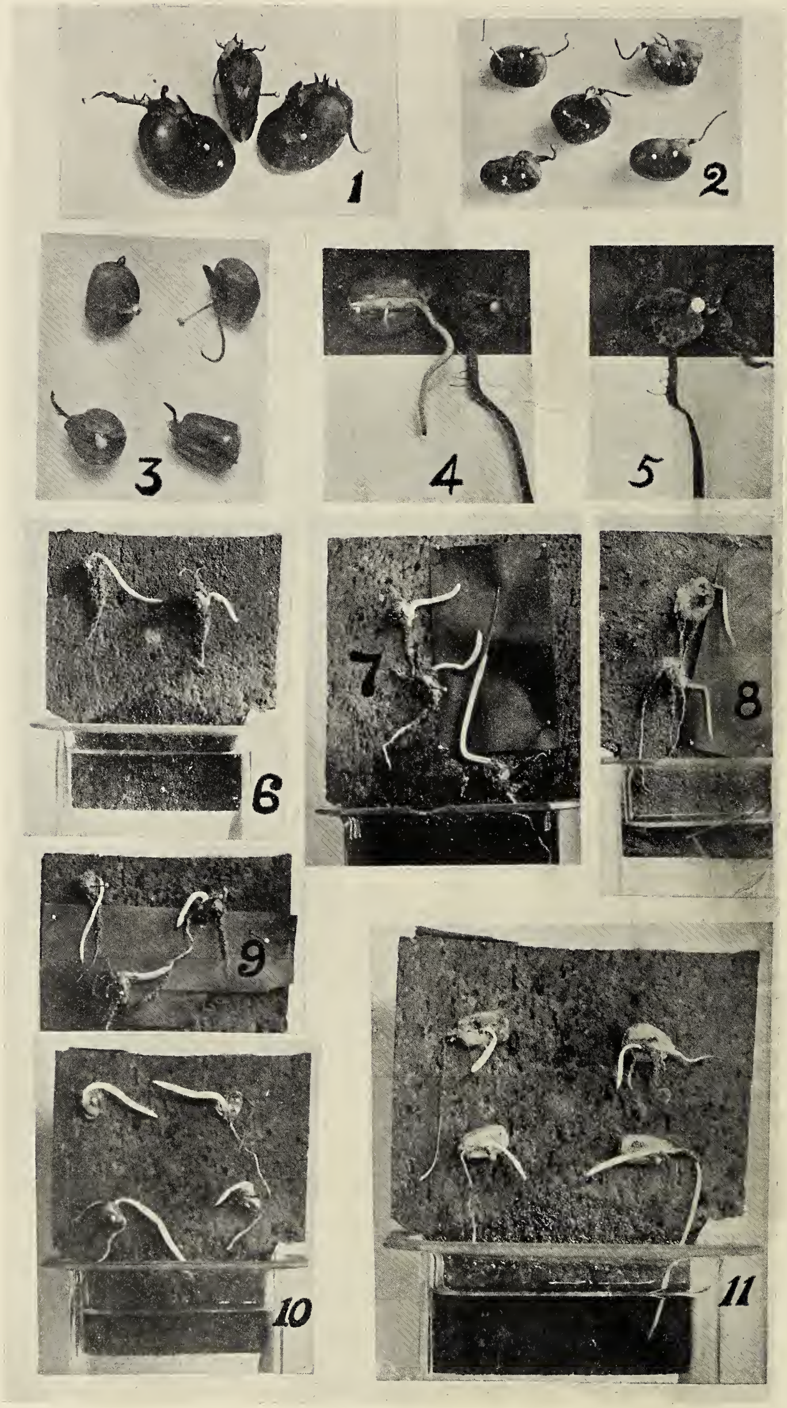

JAMES SMALL—A THEORY OF GEOTROPISM.

THE

NEW PHYTOLOGIST

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[PUBLISHED MAY 18TH, 1920.]

A THEORY OF GEOTROPISM:

WITH SOME EXPERIMENTS ON THE CHEMICAL REVERSAL OF GEOTROPIC RESPONSE IN STEM AND ROOT.

BY JAMES SMALL, D.Sc. (LOND.)

Professor of Botany, Queen's University, Belfast.

[WITH PLATE I AND FIVE FIGURES IN THE TEXT.]

CONTENTS.

CERTAIN theoretical considerations have led to the conclusion that the difference in the responses of the stem and the root under the stimulus of gravity depends upon the relative[1] alkalinity of the continuous phase of the plasma membranes of the stem apex and the relative acidity[1] of the corresponding medium in the root apex.

The experimental evidence for this view and the theoretical considerations involved, form the substance of the present contribution.

[1] "Relative," that is, to the isoelectric point of the protein or other particles of the disperse phase of the plasma membrane.

Preliminary Theories.

In an endeavour to find an explanation of the difference in the increase of electrical conductivity shown by the upper and under sides of a horizontally placed root (18-19), certain hypotheses were used. These included as a corollary a preliminary explanation of the difference in the geotropic response of stem and the root.

Hypotheses.

1. The increase in electrical conductivity is due to increased permeability of the protoplasm to ions. This hypothesis is supported by the work of McClendon, Osterhout, Stewart and Waller (see 12, pp. 103, 122), and particularly by that of Clowes (2-3). In spite of the criticism by Stiles (22) of the "assumption" that conductivity is a measure of permeability, this "assumption" is very widely used and very strongly supported by experimental evidence. The work of Höber and others makes it seem probable that "the chief impermeable layer of all cells is the plasma membrane" (12, p. 92). Lillie (11) also states that it has been found that the process of stimulation is always accompanied by an increase in permeability and probably is often dependent upon it.

2. The increased permeability was assumed to give decreased turgor.

3. The protoplasmic layer governing the permeability was assumed to contain rapidly moving (*i.e.*, exhibiting the Brownian movement, cp. Price, 16, p. 602-3) colloidal particles of a protein nature. This layer is probably of a suspensoid structure (*i.e.*, at least partly denatured) rather than of a purely emulsoid character.

The protoplasm was conceived to be an emulsion of protein or protein-lipoid particles in a colloidal protein medium. It has been shown by Fischer (4) and confirmed by Roon and Oesper (17) that a hydrated colloid is an essential part of an emulsion. It has also been shown by Fischer (4) that, while neutral casein is not a good emulsifying agent, alkaline or acid casein emulsify equally well, either becoming the hydrophilic colloid necessary as a dispersing agent.

The permeability was considered to depend on adsorption of the ions and salts by the active particles and not to be a chemical phenomenon as suggested by Stiles (21) nor a more or less static phenomenon as suggested by Fischer [(5-6), and cp. Henderson (10)] and Free (7) and Tolman (23)[1]. It was considered to be kinetic and dynamic.

[1] The views of the last author on the influence of the H-ion concentration and amphoteric colloids are very similar to those outlined below. The differences are those between a spongy structure which would not be affected by gravity and an emulsion which creams under the influence of gravity and centrifugal force. The latter is the structure observed by Price (16).

4. The semi-permeable membrane was assumed to be polarised. This is a generally recognised phenomenon (see 12, pp. 106-120).

5. The polarisation was assumed to be due, in part at least, to the electric charges on the protein particles (see 12, pp. 123-124). Proteins are known to be amphoteric colloids which are electropositive in acid media and electronegative in alkaline media. But many proteins, such as albumins and globulins, are more acid (electronegative) in themselves than basic; to render such proteins electropositive, requires therefore, a H-ion concentration (or acidity) greater than that of the protein itself.

6. The difference in the geotropic response of stem and root was supposed to be due to a difference in the charges of the protein particles in these two organs. The continuous phase of the plasma membrane in the root was supposed to be acidic beyond the PH of the isoelectric point of the protein or protein-lipoid particles of the disperse phase of the membrane. The corresponding phase of stem plasma membranes was supposed to be of an acidity below the PH of the protein particles, *i.e.*, on the basic side of the isoelectric point of the protein. The particles of the disperse phase of the plasma membranes in the perceptive region of the stem would then be electronegative; while the particles of the disperse phase of the plasma membranes in the perceptive region of the root would be electropositive.[1]

7. "There is abundant evidence to show that the plasma membrane in the resting condition is electrically polarised, and that increase in permeability reduces this polarisation" (12, p. 149). That reduction of the polarisation as such gives an increase in permeability seems probable from many investigations on the effect of acids, alkalies, salts and other substances on the permeability of both plant and animal cells.

Explanation of the Difference between the Upper and Under Sides of a Horizontally Placed Root.

With these hypotheses an explanation is suggested for the differential action of gravity on the upper and under sides of a root when it is placed horizontal. Considering the diagram (Fig. 1) the change in the polarisation of the cells in the perceptive region is supposed to affect each cell to the same extent but in an unequal or one-sided manner, *i.e.*, the amount of the change is the same in

[1] Haas (9) has shown that no acid or acid-forming substance other than CO_2 is excreted by the living root, and it seems probable from preliminary experiments that the CO_2 balance in stem and root is the chief factor governing the differentiation in hydrogen ion concentration.

in each cell but the lower side of the cell becomes differentiated from the upper side. The change is visualised as the "creaming" of the suspensoid protoplasm[1]; the electrically charged particles are supposed to ascend and thus decrease the polarisation of the lower side of the cell, while increasing the polarisation of the upper side of the cell to an equal and opposite extent.

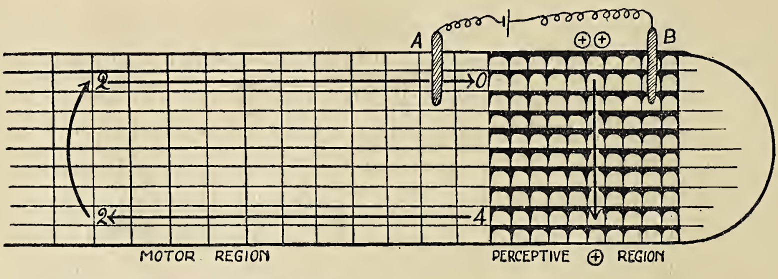


FIG. 1. Diagram of root-apex.

The more highly polarised surfaces are the upper ends of the cells while the lateral surfaces are increasingly polarised from bottom to top. Reduction in polarisation involves increase in permeability and decrease in turgor, and since these are relative terms, increase in polarisation involves decrease in permeability and increase in turgor.

In the erect position the asymmetric polarisation of the cells has no apparent effect because these regions of different polarisation are symmetrically arranged around the axis of the root. Any electric current developed as the result of the potential differences between upper and lower surfaces of the cells must likewise flow symmetrically, either down the centre and up the cortex or up the centre and down the cortex. The longitudinal growth of the root might be explained in this way.

In the horizontal position the asymmetric polarisation of the cells is arranged as in the diagram (Fig. 1). Even single cells are now recognised to be concentration cells with a definite though small electromotive force. This EMF in the normal resting condition is considered to be developed between the negatively charged outer layer and the inside of the cell which has a lower potential. In the root the outer layer was supposed to differ from the normal case in being electropositive instead of electronegative

[1] This "creaming" is dealt with very fully for particles of greater density the medium by Perrin (15). The laws governing the creaming of particles of lesser density than the medium are the same. The perceptive region and motor region differ in the height available for the creaming which is governed by Stoke's Law.

(see hypothesis 6). In the case of the vertical root there would be not only a reversed normal EMF, but a definite EMF developed as a result of the greater positive polarisation of the upper surface of each cell in the perceptive region, giving a difference of potential between the upper and lower ends of the cell. For one cell this EMF would be small, but the cells may be regarded as connected in parallel (laterally) and in series (longitudinally); the EMF would, therefore, be something quite appreciable (several hundred millivolts). The arrangement of these concentration cells and consequently of any current developed is symmetrical about the axis of the *vertical* root and no curvature would be produced.

When the root is placed horizontally the potential differences are no longer arranged symmetrically about the axis of the root. There is a higher potential (because of the "creaming" and greater polarisation) on the upper side of each cell and therefore an EMF is developed which produces a current flowing from the upper side to the lower side of the perceptive region of the root (Fig. 1). This may be described as an "action" current[1] and, on account of the resistance in the circuit, it will produce its maximum effect in the under side of the root.

One effect of the current is naturally the lowering of the polarisation of the cells giving a greater increase in permeability to ions and in conductivity in the under side of the root than in the upper side.

This current is developed in the sensitive, perceptive root apex and may be considered to be the cause of the stimulation of the cells of the motor regions. This electrical stimulation of the cells of the motor region would be, as shown above, greater in the under side; this would produce a greater increase in the permeability of the under side than of the upper side, giving greater relative turgor in the upper side and therefore greater growth of that side. The downward curvature of the root and the decrease in the rate of growth under geotropic stimulation are, therefore, explained, together with the variations in conductivity found.

It should be noted that for the effect to be greatest in the under side the outer surface of the plasma membrane is supposed to be electropositive, because the particles of the disperse phase which produce the polarisation are enclosed by a continuous phase which is acidic beyond the isoelectric point of the protein particles.

[1] Bose (1) has recorded data which prove that potential differences, such as would occur in this case, do exist in the stimulated root and stem.

Explanation of the Upward Curvature of the Stem.

According to hypothesis 6 the protein-lipoid particles of the disperse phase of the plasma membranes in the perceptive region of the stem apex are electronegative (instead of electropositive as in the root) because the continuous phase of the plasma membranes in that region is of an acidity less than that of the proteins concerned. The medium or continuous phase is not necessarily or even probably alkaline, but it is supposed to be on the basic side of the isoelectric point of the proteins and is probably slightly acid.[1]

In the perceptive region of the vertical stem there is the same creaming effect as in the root, giving a symmetrical distribution of polarised areas as in the vertical root, but the polarisation of the upper and lower surfaces of the cells is arranged in the opposite way to that in the root. The upper ends instead of being of a

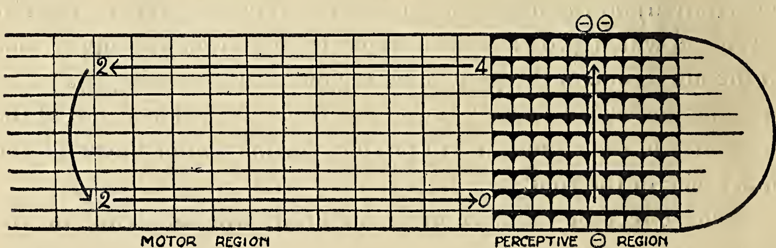


Fig. 2. Diagram of stem-apex.

higher electropositive potential than the lower ends of the cells are of a higher electronegative potential. This gives an arrangement of potential differences which are symmetrical about the axis of the vertical stem, and may at the same time account for some of the polarity of growth shown by the rootless, subaerial cryptogams.

When the stem is placed horizontally these potential differences again cease to be symmetrically arranged about the axis. The potential differences produce an EMF which gives a current from the under to the upper side of the perceptive region (Fig. 2); the direction of the current in the stem is the reverse of that in the root. Resistance is present in the stem as in the root, therefore the greatest effect will be produced in the upper side. The effect of the current on the cells of the motor region will again be an increase in the permeability, which will be greatest in the upper

[1] The H-ion concentration of plant cells as shown by Haas (8) varies in the cases he investigated from PH 3 to PH 8 (PH 7 being the true neutral point), while the PH of proteins as given by McClendon (12, p. 77) varies from 3·52 to 9·3, the majority and especially the plant proteins varying only from PH 4 to PH 5·5. The H-ion concentration of at least some plant proteins is therefore such that the variation actually found in the acidity of plant cells would be sufficient to produce electropositive and electronegative protein particles.

side. The turgor of both upper and under sides of the motor region will, therefore, be reduced, but that of the upper side will be reduced more. Growth will then be greatest on the under side and the stem will curve upwards. The distribution of these electrical effects in the perceptive and motor regions accounts for the fact that, although these two regions may be well defined, there is frequently a curvature which extends from the perceptive region to the comparatively distant region where the chief motor response takes place.

These preliminary theories having been sketched out towards the end of the year 1918, some time was spent in considering which of the many experiments they suggested would be most critical and at the same time convincing; something that could easily be repeated was desired because of certain criticisms of the excessively careful and expert manipulation required for the repetition of the previous experiments (10) on the changes in conductivity under geotropic stimulation.

It was finally decided that, if the reaction of the continuous phase of the plasma membranes in the perceptive region of the stem was really on the basic side of the isoelectric point of the disperse phase, and that of the corresponding medium in the root was really on the acidic side of the isoelectric point, it might be possible to reverse the relations of the reactions of these regions to the isoelectric point. To state the matter in more widely familiar but somewhat misleading terms—taking the isolectric point of the proteins concerned as neutral, the stem growing up because it is of an alkaline nature should grow down if its reaction is changed, while the root growing down because it is of an acid nature should grow up if its reaction is changed. There was, of course, a considerable doubt as to whether the protoplast would continue to function and reversal of the actual curvature was as much as could be expected.

This critical experiment was chosen because it seemed essential to the whole theory to suppose a real difference in the *kind* of charge on the particles of the disperse phase and at the same time an electropositive polarisation of the plasma membrane seemed to be the only point which was at variance with accepted views on the electrical conditions of the cell. These accepted views being based chiefly on animal cells, and no critical experiments having been carried out on the contrasted tissues of stem and root, there was a

possibility of something being added to our knowledge of polarisation in plants. At the same time the experiments seemed to involve no special technique and, if successful, could be repeated by anyone.

Experimental.

The experiments on the problematical reversal of geotropic curvature in stem and root were commenced in May, 1919, and the methods will now be described.

Geotropic Response of the Root.

The primary roots of *Vicia Faba* were studied first. Roots from one to two inches long were used. It was found that excess of ammonia vapour rapidly turned both testa and root quite black; the roots excreted a clear liquid and shrivelled within a day or two. With very dilute ammoniacal water it was found that the vapour was too strong the first day and had all been given off within three days. In order to get a more or less constant supply of ammonia vapour at a low concentration the following procedure was

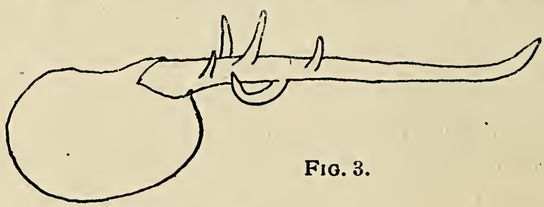
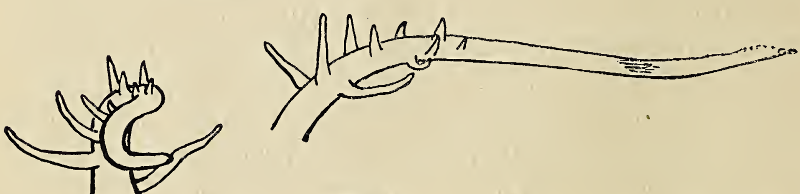


Fig. 3.



a. Fig. 4, *b.*

Figs. 3-4. Secondary roots showing reversed geotropism; Fig. 3, five rootlets; Fig. 4a, ten rootlets, end view; Fig. 4b, ditto, side view.

adopted—a piece of sheet cork was fitted into a flat museum jar so that about one third of the cork was below the level of the liquid filling the jar. The jar was filled with ammonia solution (·880) diluted to 1 in 10 with water. This was placed under a bell jar and allowed to stand for a few days; the ammonia was thus absorbed by the cork. The liquid in the jar was poured off and the jar was refilled with successive lots of tap water at intervals for about a month; the effect of the atmosphere under the bell jar on germinating beans was observed, until the vapour acquired the proper low concentration of ammonia. At this stage the vapour turned red litmus paper blue in about half-an-hour and, although

no smell of ammonia could be detected, a germinating bean pinned to the cork above the liquid had its testa blackened after two days.

With this very slightly alkaline atmosphere various experiments were carried out by pinning the seedlings to the cork above the liquid. In all cases both with *Vicia Faba* and *Zea Mays* controls were grown pinned to cork above a jar of tap water, the whole under a bell jar. These showed the normal responses. The roots in the alkaline atmosphere grew up as shown in figures 1—5, Plate I and Text-Figs. 3-4.

Many more roots were grown in an alkaline atmosphere and while many failed to show the upward curvature, none grew downwards.

These experiments may be taken therefore as preliminary confirmation of hypothesis 6 in so far as the root is concerned. On account of the susceptibility of the plants to alkaline vapour and the growth of fungi after two or three weeks, the experiments with roots were not as satisfactory as those with stems. Direct determinations of the H-ion concentration of the protoplasm of the root apex and stem apex are being attempted, but it should be pointed out that the PH of the sap is not necessarily that of the plasma membrane. The reversal of curvature is considered to be the best test devised at present because in the case of reversed curvature we are dealing with that part of the mechanism which produces normal curvature.

Geotropic Response of the Stem.

In the first stages of experimentation bean seedlings with stems one to two inches long were pinned to cork above water containing about 1% of acetic acid, under a bell jar. No geotropic response was obtained and the stems excreted liquid in the same way as the roots did in an alkaline atmosphere, they afterwards became blackened also but not to the same extent as did the roots.

The best results were obtained with the coleoptile of the maize seedling. The ordinary variety was used for most of the coleoptile experiments, but Sutton's White Horse-tooth variety reacted with equal, if not greater, readiness. The seedlings were grown in moist sand in shallow porous dishes. They were transferred to the cork when the coleoptile was about an inch long and before the first leaf emerged. Controls were grown above tap water, and acetic acid was used as before to obtain an acid atmosphere. It was found that the concentration of the acid could be varied within wide limits and an atmosphere distinctly acid to litmus paper was easily

obtained. Proceeding as before a number of experiments were carried out, with the result that the stems grew down in the acid atmosphere as shown in Figs. 6, 8 to 11, Plate I.

These experiments may be taken, therefore, as further preliminary confirmation of hypothesis 6 in so far as the stem or coleoptile is concerned. The stem has proved to be more satisfactory in the readiness with which it responds to an acid atmosphere, and because fungi do not grow so rapidly under such conditions. It is obvious that further confirmation is desirable and experiments are in progress.

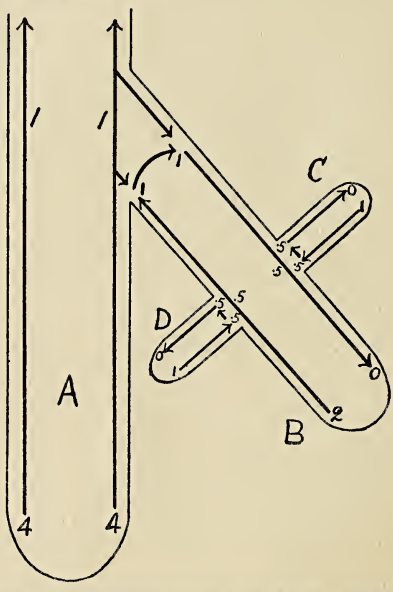


FIG. 5. Diagram to show secondary and tertiary roots.

THEORETICAL CONCLUSIONS.

After these experiments there seems to be nothing unreasonable in considering that the stem is of an "alkaline" nature with electronegative particles in the disperse phase of the plasma membrane and that the root is of an "acid" nature with electropositive particles.

EXPLANATION OF ORIENTATION OF SECONDARY AND TERTIARY ROOTS AND STEMS.

The previous theories of curvature apply only to main stems and roots. It is known that secondary roots grow at a more or less definite downward angle to the vertical under geotropic stimulation, while tertiary roots grow more or less in all directions. Secondary and tertiary stems grow in much the same way, although the

direction of growth is influenced in these cases by heliotropism, the action of which in the root system is negligible for present purposes. Any sound theory of geotropism should be able to yield an explanation of these phenomena with much the same type of protoplasm in the laterals as in the main axes.

Considering first the secondary root B of the primary root A in Fig. 5. According to previous theorisings and experiments we can suppose that a current flows upwards in the cortex of the primary root A as a result of the creaming and potential differences in the apical meristem, which should be present even in the erect root according to the views expressed above. This current being symmetrically arranged produces no "action" current and no curvature. The PD on account of the resistance will decrease as it passes upwards, see Fig. 5, where the PD is supposed to be reduced from 4 to 1 at the base of the secondary root B.

If the secondary root B were placed horizontally it would develop asymmetric potential differences, an EMF and an action current as outlined for the horizontal primary root. Since the meristem is smaller the current would be smaller but it would still have a greater effect in the lower side and the rootlet B would tend to grow vertically downwards. At the point where it joins the primary root A, however, there is a current flowing in the cortex which would enter the rootlet B both in the upper and the under sides, if the potential differences were suitable. This "leakage" of the normal polarity current from A would tend to flow towards the apex of B; in the under side it would meet an opposing current, while in the upper side it would flow or tend to flow in the same direction as the action current of B. The action current and its effects in the upper side of B would, therefore, be augmented by the normal polarity current from A, while the action current in the under side of B would be more or less reduced by the normal polarity current from A, according to the relative potential differences of the current from A and the current in B at the point where it meets the primary root A.

The general effect of the current from the primary root would thus be to neutralise more or less the asymmetric effects of the action current in B, and *the angle at which the asymmetric effects of the action current in the secondary root are neutralised by the leakage of the normal polarity current from the primary root is the angle which the secondary root will make with the vertical.*

An angle which was greater than the angle of balance would increase the strength of the action current and the rootlet would grow downwards. An angle which was less than the angle of balance would result in reversed asymmetric effects from the action of the normal polarity current from the main root and the rootlet would grow upwards.

This stable angle is known to be very much the same when the root system is inverted. Under these conditions the primary root would also be inverted vertically and the current would be similar in strength but different in direction of flow in the primary root; it would still tend to flow into the secondary root. The action current in the secondary root would also be reversed in its relation to the morphologically upper and under sides so that the balance would again be reached when the secondary root had attained the same angle with the vertical as before and, therefore, had the same strength of action current.

It is not necessary to labour this point. Many experiments and observational details in connection with secondary roots are clearly to be explained along these lines, always keeping in mind the point that if the primary root is at an angle to the vertical there will be an *action current* in it, instead of a *normal polarity current*, which may so augment the effects of the action current in the secondary root that it (the rootlet) will curve away from instead of towards the vertical until it has developed an action current sufficiently strong to balance once more the current "leaking" from the primary root.

Considering next the tertiary roots C and D of the secondary root B, the electrical conditions are becoming rather complex. These tertiary roots arise on all sides of an organ which is no longer symmetrical physiologically about its own axis, as in the case of the primary root. Although the total effect in the upper and under sides may be the same with B at its angle of balance, the asymmetric PD is still there. The lateral sides of the secondary root would be in similar electrical condition, but that condition would not be the the same as upper and under sides. There would be a great variety of current strengths in the secondary root which would require to be balanced by the action currents of the tertiary roots before these could reach a stable angle. Taking C and D as examples of such tertiary roots, D would reach its angle of balance when the unilateral effects of its action current (PD 1 in Fig. 5) were neutralised by the inflowing current (PD ·5 in Fig. 5) from B; and C would behave in a similar fashion although in that case the angle of balance would be unstable.

Since the action currents at the angles given in the diagram (Fig. 5) would be somewhat similar in strength (cp. Newcombe, 14, for primary roots), and their effects would be neutralised by the same current strength (PD ·5 in Fig. 5) from both upper and under surfaces; these angles would be the angles of balance and C would grow upwards and D downwards. If C had a downward angle the same as that of D it should theoretically grow downwards but it arises on the upper side and is thus directed upwards before it has developed the motor region which is necessary for geotropic curvature.

Secondary and tertiary stems can be treated theoretically in the same way, always keeping in mind the point that the action current in the lateral branches and the normal polarity current in the main stem are to be considered as reversed in their direction and arrangement as compared with those in the root, so that the secondary laterals take up an upward angle of balance. The actlon of heliotropic stimulation interferes chiefly with the angles of the tertiary branches, because in these the geotropic action currents are weak compared to those of the main stem and secondary branches.

The action of heliotropic stimulation becomes altogether predominant in the leaf, which may be regarded as neutral or non-polarised as far as gravity is concerned. Buds, flowers and fruits show gravity responses (13, etc.), but the responding region is usually the stalk which can be regarded as a secondary or tertiary stem structure. Food supplies also may interfere in such cases by altering the osmotic pressure, apart from permeability changes, as has been suggested previously (20, pp. 197, 295).

Although this theory of geotropic stimulation and curvature in stem and root thus explains the chief points in the orientation of stems and roots in normal and in experimental conditions, and the orientation of their secondary and tertiary laterals, and although it is also in complete accord with the known facts of the physico-chemical phenomena of protoplasm and cellular tissues, it is recognised that a large field for experimental work is opened up in the verification of details and in the development of the new measure of control over the plant organism which is suggested.

As a theory the suggested differentiation in hydrogen ion concentration of root and stem has very wide applications to cytolysis, acid-tolerant and calcifuge species, immunity from and liability to attack by bacteria and fungi, the development of

intumescences, the effects of acids, alkalies and salts on plants and animals in general and on the permeability of protoplasm in particular and possibly also to epharmonic variation. It provides an explanation, not only for the normal polarity of growth in plants, but also for the changes in geotropic response and in colour which occur in flower buds and other organs. The adsorption of ions by the Brownian particles, which is postulated, furnishes an explanation of the stimulus/response ratio of the Weber Law as modified (24-25) by Waller.

EXPLANATION OF PLATE I.

Fig. 1. Three beans with secondary roots showing negative geotropism.

Fig. 2. Main roots of the bean showing the same.

Fig. 3. Main roots of the maize showing the same.

Fig. 4. Adventitious roots of the maize ; two show slight upward curves.

Fig. 5. The same, five days later, with more pronounced upward curves.

Fig. 6. Maize stems with unbroken coleoptiles showing positive geotropism.

Fig. 7. Controls in a neutral atmosphere : the top specimen has recovered after growing down as in Fig. 6. (specimen on the right).

Fig. 8. Maize stems, showing cytolysis and fungal infection after downward curving had taken place.

Fig. 9. Maize stems showing positive geotropism, the lower specimen did not react at all, either positively or negatively.

Fig. 10. Three of four stems showing the same.

Fig. 11. Four stems all positively geotropic.

BIBLIOGRAPHY.

1. Bose, J. C. Plant Response. London, 1906.
2. Clowes, G. H. A. On the electrical resistance and permeability of tumour tissues. Proc. Soc. Exp. Biol. and Med., 15, p. 107 1918.
3. ,, ,, On the action exerted by antagonistic electrolytes on permeability of emulsion membranes. Ibid, 15, p. 108, 1918.
4. Fischer, M. H. and Hooker, M. O. Physical Chemistry of Emulsions. Science, 43, p. 468, 1916.
5. Fischer, M. H. On the swelling of gelatin in polybasic acids and their salts. Jour. Amer. Chem. Soc., 40, p. 272, 1918. See also Science, 46, p. 189, 1917.
6. ,, ,, The colloidal-chemical theory of water absorption by protoplasm. Jour. Amer. Chem. Soc., 40, p. 862, 1918.
7. Free, E. E. A colloidal hypothesis of protoplasmic permeability. Plant World, 21, p. 141, 1918.
8. Haas, A. R. The Acidity of Plant Cells as shown by Natural Indicators. Jour. Biol. Chem., 27, p. 225, 1916.
9. ,, ,, The excretion of acids by roots. Proc. Amer. Nat. Acad. Sci., II, p. 561, 1916.

10. Henderson, L. J. and Cohn, E. J. On the swelling of protein colloids. Jour. Amer. Chem. Soc., 40, p. 857, 1918. (Fischer's reply, ibid p. 862; Henderson's counter reply, ibid p. 867).

11. Lillie R. C. The Rôle of Membranes in Cell Processes. Pop. Sci. Monthly, 82, p. 132, 1913.

12. McClendon, J. F. Physical Chemistry of Vital Phenomena. Princeton Univ. Press, 1917.

13. Möbius, M. Movements of orientation in buds, flowers and fruits. Flora, 111-112, p. 396, 1918.

14. Newcombe, F. C. Geotropic response at various angles of inclination. Ann. Bot., XIX, p. 311, 1905.

15, Perrin, J. Brownian Movement and Molecular Reality. Eng. trans. London, 1910.

16. Price, S. R. Some Studies on the Structure of the Plant Cell by the Method of Dark-ground Illumination. Ann. Bot., XXVIII, p. 601, 1914.

17. Roon, L. and Oesper, R. E. Theory of Emulsification based on Pharmaceutical Practice. J. Ind. Eng. Chem., 9, p. 156, 1917.

18. Small, J. Geotropism and the Weber Law. Ann. Bot., XXXI, p. 313 1917.

19. ,, ,, Changes of Electrical Conductivity under Geotropic Stimulation. Proc. Roy. Soc. Lond., B. 90, p. 349, 1918.

20. ,, ,, Origin and Development of the Compositæ, NEW PHYTOLOGIST Rep. XI., 1919.

21. Stiles, W. and Jörgensen, I. The effect of Temperature on the Permeability of Plant Cells to the Hydrogen Ion. Ann. Bot., XXIX, p. 611, 1915.

22. Stiles, W. Irritability. Science Progress, Vol. XIII, No. 51, p. 395, 1919.

23. Tolman, R. C. and Stearn, A. E. The Molecular Mechanism of Colloidal Behaviour. I. The swelling of fibrin in acids. Jour. Amer. Chem. Soc., 40, p. 264, 1918.

24, Waller, A. D. Points relating to the Weber-Fechner Law. Brain, 1895, p. 205.

25. ,, ,, The Signs of Life. London, 1903.

MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER II.—*Continued.*

Foundations of the Mutation Concept.

FROM the standpoint of the mutation concept, *Œnothera lata*, while a critical case in demonstrating the occurrence of germinal changes, differs in several respects from the most frequent and widespread type of mutation, *i.e.*, the type which results in a new Mendelian character. The latter type of change will be considered in greater detail in connection with the origin of dominant and recessive Mendelian characters, mass mutations and parallel mutations. The type of mutation involving an extra chromosome differs from this in the following points. (1) There are present three representatives of the extra chromosomes instead of a pair. A Mendelian mutation, on the other hand, will first appear usually as a heterozygous individual if the new character is dominant, or as an individual homozygous for the new character if it is recessive: that is, a pair of chromosomes only will be involved, one or both of which carry the new factor. (2) As we shall see later, the presence of the extra chromosome determines, at least in large measure, the hereditary behaviour of the form possessing it. (3) Chromosome duplication, viewed as a germinal change, arises through, or at least in connection with, a rearrangement of the chromatic material, resulting from an irregular distribution or non-disjunction of a pair of chromosomes in the heterotype mitosis, while when a Mendelian character arises one must assume it is by an alteration in one element of a chromosome.

Thus while the bearing of the extra chromosome in *Œnothera lata* upon the mutation concept is clear in that, as we have already pointed out, there is a constant relation between the *lata* characters and the additional chromosome, yet the relation of this type to the numerous other forms now known to have 15 chromosomes is by no means so clear, and raises a number of intricate problems. These forms and the problems connected with them will be discussed later. For the moment we are concerned in pointing out some of the other bases of present concepts regarding mutations.

The *gigas* and *semigigas* series of forms, having respectively 28 and 21 chromosomes, again clearly justify the concept of a mutation as a cell change involving a new nuclear structure perpetuated by mitosis. This type of change is now known,

through parallel mutations, in several species of *Œnothera*: but tetraploidy exists in a wide range of wild species, and a doubling of the chromosome series is also known to occur under various experimental conditions which will be referred to later. The forms, such as *lata* and *semigigas*, with an unbalanced chromosome number, will seldom if ever breed true, and such forms can only occupy a somewhat temporary and aberrant place in evolutionary descent. But tetraploidy is a condition of evolutionary significance, as the cytological study of many genera and families already shows. It gave the first hints towards the construction of a phylogeny of the chromosomes, and ultimately it is quite certain that such a phylogeny must be constructed.

While the 15-chromosome mutants produce two types of gametes, and hence are at least dimorphic in their offspring when crossed back with the parent type, the tetraploid forms are also peculiar in their inheritance, giving triploid intermediate hybrids when crossed back with the parent (diploid) type. Such forms are for the most part unstable, and although they occur in nature (*e.g.* the well known natural hybrid between *Drosera rotundifolia* and *D. longifolia*) yet their instability and partial sterility prevent their giving rise to permanent intermediate links between the original diploid species and its tetraploid derivative. Meiotic irregularities in these hybrids may lead to the production of a series of plants with new chromosome numbers, as is well known in the Œnotheras. But seldom will a stable form arise having a balanced chromosome equipment. With the exception of tetraploidy, therefore, none of the types of visible chromosome change so far demonstrated in the Oenotheras are likely to have played a very large rôle in any phylogeny. They are chiefly valuable as a means of furnishing a visible demonstration of the occurrence of germinal nuclear changes.

All the evidence indicates that the great mass of mutations originate as new Mendelian characters. Among such changes in the Œnotheras are *Œ. rubricalyx*, a dominant, and *Œ. gigas nanella*, which in crosses with its parent form *gigas* behaves as a Mendelian recessive. We may consider these two forms as types of Mendelian mutants. On the basis of their inheritance as such, we must assume that they originate through an alteration in a particular locus of one chromosome, a view set forth elsewhere[1] and now generally accepted. The history of *Œ. rubricalyx* has been given in the work cited,[2] but the salient points may be referred to here.

[1] The Mutation Factor, p. 300.

[2] The Mutation Factor, p. 102.

One plant in a large culture of *Œ. rubrinervis*[1] appeared with an extreme increase in anthocyanin pigment, this red being especially conspicuous on the sepals, flower stalk, stem, and the under surface of the leaves, although histological examination shows it to be present in increased quantity in all parts of the plant. The original individual was heterozygous, originating therefore through the union of a mutated with a non-mutated germ cell. The premutation must then be considered to consist in a change, probably chemical, in a locus of one chromosome, and this change probably occurred during some stage of meiosis. Farther than this the matter cannot be analysed at present. The altered chromosome, present in the nucleus of every cell through mitosis, increases the capacity of every cell for producing anthocyanin, as is shown for instance by comparing cells of the chalaza in the two forms.

Through an unfortunate accident, only a few offspring of the original *novum* survived. They were 9 *rubricalyx*, 1 *rubrinervis*, and 2 rosettes classed as "doubtful." The next generation gave three families, with ratios 10 : 5, 14 : 6 and 33 : 11 respectively, all clearly representing 3 : 1 families. This leaves no reasonable doubt that the original *rubricalyx* mutant was heterozygous for one factor for red. For by no possibility can any of the three ratios 10 : 5, 14 : 6 or 33 : 11 be considered to represent a 15 : 1 ratio, while their total, 57 ; 22, is clearly close to the 3 : 1 expectation. Also the ratio in the previous generation (which may be taken as probably 11 : 1), from which these three families were derived by selfing certain individuals, while it might by itself conceivably represent a 15 : 1 family, cannot do so really. Because the chances are remote that, if the parent mutant were heterozygous for two factors for red, three of its offspring taken at random as mother-plants of the next generation should all happen to be heterozygous for a single factor (therefore giving 3 : 1 ratios) and none of them homozygous or heterozygous for two factors.[2] The evidence taken as a whole is therefore clear that *rubricalyx* originated in one individual which was heterozygous for a single factor for red.

[1] It now appears (Lutz 1917b) that the form which other investigators, at least MacDougal, Miss Lutz and myself, regarded as *rubrinervis*, differs from the Amsterdam *rubrinervis*, which is a less robust form. Further study by de Vries has revealed several types closely related to *rubrinervis*, which will be referred to later.

[2] If the original mutant were heterozygous for two factors for red, it would give in its offspring 1 plant which bred true to red, to 8 yielding *rubricalyx* and *rubrinervis* in the ratio 15R : 1r, to 6 yielding ratios 3R : 1r, to 1 pure *rubrinervis*. It gave in fact three families all of which were 3 : 1.

Duplicate Factor Mutations.

This fact is thus emphasized because later generations produced some families with 15 : 1 ratios, hence representing two factors for red, in addition to families with 3 : 1.[1] Furthermore, certain 15 : 1 families came from members of families showing a 3 : 1 ratio.[2] These must therefore have been due to secondary mutations. The evidence, part of which has been considered elsewhere,[3] shows with a high degree of probability that, as we have seen, the original mutant was heterozygous for a single factor for red. Shull (1914a), unfortunately, from a study of hybrids between *rubricalyx* and *Œ. grandiflora* which he mistook for pure *rubricalyx*, drew erroneous conclusions regarding the origin and behaviour of this striking form. Another important feature in its history, already mentioned, is the fact that members of a family of *rubricalyx* which contains a single factor for red, as shown by the 3 : 1 ratio, can give rise to individuals which are heterozygous for two factors for red. How this may come about has been discussed under the name duplicate mutation[4].

That two or even three factors for the same character may exist in a given strain, was first shown by Nilsson-Ehle (1909) for wheat, and has since been demonstrated in a number of other forms. Nilsson-Ehle showed for example that while Extra Squarehead wheat has only one factor for red kernels, Sammet and Grenadier have three, and in a later paper (1911) that Swedish Binkel has two. A list of such duplicate determiners has been given by Shull (1914b). It includes glume colour, hairiness of glumes, length of glumes, width of leaves, etc., in oats, and various characters in beet, turnip, gourd, flax, tobacco, bean, pea, velvet bean, wheat, and maize among plants ; also body weight in ducks, fecundity in fowls, skin colour in man, ear length and body size in rabbits, piebald coat colour in mice and the hooded pattern in rats. Of course some of these cases are much better substantiated than others, and the number of cases has since been considerably increased. The Howards (1912) have demonstrated one of the clearest cases of duplicate factors for red in wheat.

Nilsson-Ehle did not consider the origin of this condition of duplicate factors in wheat, but it appears probable that it has the

[1] Gates 1915b.

[2] Some 5 : 1 ratios were also obtained, which are probably to be explained by linkage.

[3] Gates 1915e.

[4] Gates 1915b.

same explanation as the duplicate condition of the factor for red in *Œ. rubricalyx*. There are, as previously pointed out[1], at least two ways in which such a result is likely to have come about. (1) Through a locus in a second chromosome having independently undergone the same change or mutation. (2) An individual which would normally be homozygous for one factor for red (RR′) might, by a mismating of the chromosome pairs in fertilization or after, become heterozygous for two factors for red (RrR′r′). In this way an individual giving a 15 : 1 family of offspring could arise from a homozygous member of a 3 : 1 family. It is necessary to assume that such a regrouping of chromosomes took place at fertilization or soon after, so that the nuclei of the whole germ track[2] would have the same chromosome grouping. The difficulty with this view, and it appears now to be a fatal one, is that it seems necessary to assume that the other chromosomes with which these two "red" chromosomes are mated will differ from them in other factors as well and will therefore introduce new differences in the offspring. Morgan has shown in *Drosophila* that eye-colours so closely alike as to be indistinguishable except by the expert, may arise in different chromosomes, as independent mutations.[3] Hence it appears more probable that these factors for red in *Œ. rubricalyx*, which are as yet quite indistinguishable, may have arisen in the same way through successive parallel mutations in different chromosomes of the same race.

Shull (1914b), however, uses the second hypothesis, mismating of chromosomes, to account for the origin simultaneously of the duplicate condition for triangular capsule form in *Capsella bursa-pastoris* and the mutant *C. Heegeri* with round capsules. If, in the reduction division, the pair of chromosomes containing each a determiner for triangular capsule pass into the same daughter nucleus, this would produce an individual with duplicate factors for capsule form, while the other germ cell, lacking both these determiners, would later give rise to the mutant *Heegeri*. His modified suggestion that both these conditions, (1) duplicate factors for triangular capsule, (2) the origin of a mutant lacking both these

[1] Gates 1915b.

[2] The term germ track, the English equivalent of the German *Keimbahn*, is used to represent the line of cells or cell divisions following each other from the fertilised egg to the pollen mother cells or the eggs. As de Vries pointed out *(Intracellular Pangenesis)*, we may thus think of a pedigree of cells derived chiefly from apical cells and forming a connected system.

[3] In the same way, the factor for red midribs described by Heribert Nilsson (1912) in a derivative of the Swedish race of *Œ. lamarckiana* appears to be different from that in the Amsterdam race.

factors and hence round, could come about through the detachment of the determiner for triangular capsule from the end of one chromosome and its attachment to the end of the next, seems more likely and more in accord with our present knowledge. The difficulty with it as a general explanation is that one cannot suppose that all duplicated factors have been conveniently located on the end of a chromosome, especially where a number have been described for the same organism, as is the case with wheat, maize and tobacco. The most likely hypothesis of the origin of most duplicate factors is then the independent origin of each through a chemical alteration of a locus in a different chromosome.

However, the recent breeding experiments with *Drosophila* have disclosed cases (Bridges 1917) of duplication in which the genetic behaviour is as though a group of genes from the middle of one X-chromosome has become attached to the end of the other X-chromosome in a female. Another exceptional case, discovered by Bridges and reported by Morgan (1919), is explained on the assumption that a piece from the second chromosome has become attached to the middle of the third chromosome. In the resulting race, when these chromosomes separate and recombine in reduction and fertilization, zygotes which receive the deficient second chromosome fail to develop unless they also receive the third chromosome with the additional (duplicate) piece. We are therefore at liberty to suppose that a redistribution of certain chromatin elements, rather than a fresh transformation of a new determiner has taken place in certain instances. But such cases will usually involve a group of factors simultaneously rather than a single one.

Recessive Mendeliau Factor Mutations.

If we turn now to *Œnothera gigas nanella* as the type of a recessive Mendelian factor mutation, the manner of its origin seems clear from its hereditary behaviour. De Vries (1915) has brought together the evidence concerning its behaviour. *Œ. gigas* produces this dwarf in 1—2% of its offspring, *i.e.*, as mutations. But certain individuals of *gigas* are known, from observations of Schouten, Gates and de Vries, to produce as many as 18% of dwarfs. Such individuals are evidently heterozygous, arising from the union of a normal *gigas* germ cell with one which has mutated so as to carry the dwarf factor instead of that for tallness. Theoretically they should give 25% of dwarf offspring but the number is reduced by their lesser viability. This phenomenon of producing in the

offspring a large number of a new form has been called by Bartlett (1915) mass mutation. In such a case it is obvious that the original change or pre-mutation, an invisible change in a germ cell, must have occurred in a plant at least two generations earlier than that in which the mass mutation exhibits itself. The 1 or 2 per cent of mutants arising from other *gigas* plants are the result of the chance meeting of two germ cells both of which have mutated so as to carry the dwarf instead of the tall condition. This interpretation is clearly substantiated by the fact that *Œ. gigas nanella* when crossed with *Œ. gigas* behaves as a simple Mendelian recessive. It has 28 chromosomes, like the parent form.

Thus it would appear that many recessive Mendelian characters originate either as single individuals from the union of two mutated germ cells, or with a frequency approaching 25% in the offspring of individuals which have in turn arisen as a heterozygous combination of a mutated and a non-mutated germ cell.

In races or species where self-fertilization is the rule, a viable recessive mutation is very likely to "come out" in two or three generations, but in many animals, including man, where a large amount of inter-crossing of strains takes place, recessive mutations may accumulate over a considerable period, and some of them may then come out as soon as in-breeding begins. Thus in the case of cross-breeding organisms, it is impossible to say, when a recessive Mendelian mutation appears, how long it may have been carried in the germ plasm in a heterozygous condition without getting a chance to express itself. The premutation may have taken place many generations earlier.

As one more case of a presumptive Mendelian mutation in *Œnothera* we may consider *Œ. brevistylis*. Although it has never actually occurred as a mutation in controlled cultures, yet the fact that it was found by de Vries growing wild with *Œ. lamarckiana* although it ripens practically no seeds, indicates that it must have been derived from *lamarckiana*, with which its pollen crosses freely. In this way it maintained itself for seventeen years. When seeds can be obtained it is shown to breed true, and the chromosomes number 14. De Vries (1913) found it to behave as a simple Mendelian recessive, and Davis (1918) confirms this from a more extensive series of crosses. He finds that the reciprocal crosses with *lamarckiana* are uniform and indistinguishable, the characters of *lamarckiana* being strongly dominant. But measurements show that in heterozygous individuals *brevistylis* has an influence in

shortening the styles, slightly broadening the leaves and bracts, making the bud cones a little thicker and the sepal tips somewhat shorter. The resulting segregation in F_2 is sharp and complete, but the percentage of *brevistylis* is usually below expectation in all crosses, owing to *brevistylis* zygotes being apparently less viable.

This is a very good example of a type which was able to survive for an indefinite period in competition with its parent form, because while producing practically no viable seeds it was perpetuated by occasional crosses of its pollen giving rise to heterozygous *lamarckiana* plants.

Mutations Arising at or After Fertilization.

De Vries assumes that all mutations take place in the formation of the germ cells, that is presumably at the time of the meiotic divisions, and there is a great deal of evidence that many germinal changes arise at this time. During this period the pairs of chromosomes are being redistributed, and the intricate manœuvres of the chromatin material just previous to this separation of the chromosomes gives an opportunity for a variety of rearrangements and aberrant distributions of particular chromatin particles. That the hereditary behaviour known as *crossing-over*, by which part of the factors which were in the same chromosome cross over to its mate, has its basis in changes occurring at this time has been shown experimentally for *Drosophila* by Plough (1917). He found that by subjecting the females to high or low temperature the amount of crossing-over was increased. Further experiment showed that the critical period, during which crossing-over in the offspring was affected, was during the period of conjugation of the chromosomes in the maturation of the eggs. From this it follows that crossing-over takes place at that time and not earlier.

In the Œnotheras it has been shown that many of the irregularities leading to new chromosome numbers arise during meiosis. The origin of mutations with an extra chromosome and the phenomena of non-disjunction in *Drosophila*, of the sex-chromosomes (failure to separate in meiosis), are cases in point; also the origin of the supernumerary chromosomes in *Metapodius* (Wilson 1909), which arise through irregularities in chromosome distribution during spermatogenesis. In addition, there is evidence both in plants and animals that germ cells with a double number of chromosomes are occasionally produced, through an alteration in the meiotic phenomena. These matters will be discussed in connection with triploidy and tetraploidy. It will be found that the

hypothesis of de Vries (1913) that triploid and tetraploid mutants arise *only* through the union of germ cells one or both of which is diploid is unnecessary, since both these conditions may arise in other ways.

The period of fertilization is an equally critical time in the life cycle of an organism, and the evidence indicates that a number of germinal readjustments or mutations date from this period. Both triploidy and tetraploidy may perhaps arise at this time or shortly after. It has already been pointed out[1] that in crosses such as *Œ. nanella lamarckiana* and its reciprocal, where both parent types split out in the F_1 generation and both subsequently breed true, it is reasonable to conclude that some determining reaction occurs in the fertilized egg, in which one parental germ cell or the other gains the ascendancy. This was formerly explained by De Vries on the basis of pangens in different conditions. But since the important work of Muller (1918) on balanced lethal factors in *Drosophila,* it is evident that linkage to such lethal factors may explain this result, though more will need to be known concerning such lethal factors in *Œnothera* before the explanation can be applied in detail. Differential sterility depending on whether the lethal factor is linked to (*i.e.*, is in the same chromosome with) the factor for dwarfness or that for tallness, would seem to meet the case.

Concerning the origin of *Œ. lamarckiana* mut. *nanella,* we may assume that it appears through the breaking of the linkage between the dwarfing factor and a lethal factor, for if it were a simple Mendelian recessive we should find occasionally a *Lamarckiana* plant which was heterozygous for dwarfness and gave 25% dwarf offspring. But such are never found in *lamarckiana* although, as we have already pointed out, they do occur in *Œ. gigas.* This suggests that *gigas* has lost some of the lethal factors present in *Lamarckiana.* As a mutant, *nanella* has a frequency of only 1—2%, so that the cross-over between the dwarf and lethal factors must be an infrequent one. The discussion of lethal factors will be taken up again later.

That mutations in other forms may date their origin from fertilization has also been held, and Punnett (1919) has recently concluded that this is the time of origin of the well-known cretin mutation in the sweet pea. This mutation differs prominently from the type in having a straight stigma protruding through a cleft

[1] The Mutation Factor, p. 222.

keel, and it is invariably sterile on the female side. It behaves in crosses with the parent as a simple Mendelian recessive, a total of 80 families in six years giving 4198 normals : 1322 cretins, which is not far removed from a 3 : 1 ratio, the viability of the cretin being evidently somewhat less than that of the normal form.

The cretin appeared in a cross between two white sweet peas, Blanche Burpee with long pollen and Emily Henderson with round pollen. From three purple F_1 plants large F_2 families were raised in 1905. From one of these F_2 families containing 187 plants, the seed of 29 individuals was saved for the F_3 generation. These 29 families in 1906 resulted in 2083 plants, all normal. Seeds for the F_4 generation were saved from 14 individuals of one of the F_3 families numbering 181 plants. The F_4 from these 14 plants gave 1118 plants, one of which was the cretin. This appeared in a family of 52 plants raised from the F_3 plant $304^6/1906$. Thirteen sister plants yielded no cretin in a progeny of over 1000, nor did one appear among the 2083 plants of the F_3 generation. The F_5 of 195 plants grown in 1912 from 9 F_4 plants, also failed to produce one, so it remains an isolated case.

Punnett points out that under these circumstances it is unlikely that the cretin originated from two germ cells, each of which had lost the normal factor, for in that case the parent plant would have been heterozygous, giving 25% cretins, and they would also have appeared in the F_5 or in collateral families. Hence he concludes, in agreement with the argument above, that the cretin plant must have arisen through " some radical alteration in the zygote after union between two normal gametes had already taken place," and that it was " due to a change in the individual at some stage *after* fertilization whereby the factor for the normal flower was either dropped out or altered during the somatic divisions." Since the germ cells of this plant were uniform, it is reasonable to suppose that the change took place in the fertilized egg itself.

Morgan (1919), in discussing this case, suggests that the mutation occurred in one chromosome far enough back in the germ track of the parent individual to give rise to pollen and ovules (say in one flower) each carrying the mutated genes. But in that case other germ cells would have been carrying these genes, and these would surely have appeared later either in the heterozygous or homozygous condition.

As regards *Drosophila*, the great number of mutants it has produced apparently all belong to one type, and behave in the same

way. They are nearly all classed as Mendelian dominants or recessives in inheritance, though in a few dominance is variable and subject to environmental influence. Morgan (1919), states that only 12 are dominant out of over 150. These dominants have each appeared in a single individual. Mutants from recessive genes, on the other hand, usually came to light in about 25% of the offspring of a pair, showing that the pair were both heterozygous for the new factor, which must have arisen at least one generation earlier. Whether both members of a pair of chromosomes undergo the change simultaneously is unknown, since if it occurred in the egg one chromosome will be extruded into the polar body, and if in the spermatocyte the chances are small that more than one sperm from the same spermatocyte will function. Still, as far as it goes, the 12 single mutant individuals suggest that perhaps a single sperm and hence a single chromosome of a pair has the new factor. In the case of *Œnothera lata* and *semilata*, which arise through an irregular heterotype division, evidence is available, for these mutants sometimes occur in pairs, suggesting that the change occurred in a pollen mother cell and that the two resulting 8-chromosome pollen grains both functioned.

Drosophila Mutations.

The evidence for mutations in animals was rather scanty until Morgan took up the study of the fruit fly, *Drosophila melanogaster*, about 1910. The rapid breeding and easy handling of these flies in large numbers, makes it an ideal form for genetic experiments, and combined with this is the advantage that it has only four pairs of chromosomes. It is not, therefore, surprising that in the last decade, Morgan and his pupils have accumulated a mass of breeding data, closely analyzed and correlated, which is unequalled in any other organism. With plants growing only one seed-generation a year, it would probably require 150 years to produce an equal number of generations.

The *Drosophila* work has therefore given us a look into the constitution of the germ plasm such as no annual-breeding plant or animal could furnish in a lifetime. The Mendelian behaviour, sex-linked inheritance, and other features are similiar to those found in many other organisms, so there can be no doubt of the wide applicability of the conceptions of mutations and the germ plasm derived from these experiments. In many respects they are in accord with those derived from the *Œnothera* work. Although the simple Mendelian mutations in the latter are comparatively

few, we have already seen that the behaviour of the others can probably be accounted for on the basis of sterility or lethal factors, explanations which now enter into many features of the Œnotheras. Again, the duplication of a chromosome in *Œ. lata* and other forms is paralleled by the phenomena of non-disjunction in *Drosophila*, although there are certain differences which will be pointed out. But in *Drosophila* the rapidity in breeding large numbers in many generations has made it possible to carry the analysis of the germ plasm much further than in any plant.

In the single species *Drosophila melanogaster*, the "vinegar fly," over 150 mutations have been observed. These include more than 25 factors for eye colour, and many more for body colour and form of wings, while many structural differences are also involved in other mutations. The majority of these have appeared but once. Some mutations are, however, more frequent. White eyes, a mutant from the wild red-eyed fly, are known to have occurred three times in the New York experiments (Morgan, 1919, p. 248) and several times in the cultures of other observers. Vermilion eye-colour has appeared at least six times, "rudimentary" wings five times, cut wing four times, truncate wing frequently but probably owing to different changes. As with the *Œnothera* experiments then, certain mutations repeat themselves, but apparently with much less frequence. This suggests that in *Œnothera* the mutation often appears much later than the germinal change (pre-mutation) which gave rise to it, being suppressed in many cases by lethal factors causing sterility.

A number of cases of probable reversion from the mutant character to the original wild type have occurred, but most of these are uncertain on account of the possibility of contamination. In the experiments of May (1917a) with bar-eye, however, this possibility is excluded. This character is dominant to normal (round) eye, and the reversal takes place with sufficient frequency to eliminate the possibility of error. Reverted individuals give only normal offspring. Bar-eye differs from the normal in having fewer facets, and the stock showed considerable variability. In an experiment in selecting for more or fewer facets, May obtained six full-eyed males and five females heterozygous for full-eye. They were indistinguishable from normal and were explained as simple reverse mutations. In a later paper (May 1917b), however, a more complex explanation of this reversal is favoured. It is assumed that the normal wild fly carries a limiting factor with respect to

facet number, and that by "partial non-disjunction," the factor passes from one chromosome to another (presumably during meiosis) so that one chromosome is without a limiting factor while the other member of the pair has two. The egg retaining the latter chromosome would produce a bar-eyed individual. If in such a race a second non-disjunction occurs, separating the two factors, one chromosome would result having triple factors and one with a single factor. The latter would give a reversion to a full-eyed male or a heterozygous female. But it is doubtful if such a method of explanation by splitting up the factor could be applied to reversions in other factors which show no such variability as bar-eye.

A chemical reversal seems more likely to supply a general explanation of reverse mutations, and this is important in its bearing on the nature of a mutational change. For if a recessive mutant factor can revert to the wild condition, then the mutation was not due to an irrevocable loss of a particle, but rather to the transformation of a particle or locus of a chromosome, first in one direction and afterwards back to the original condition.

As regards the infrequency of simple Mendelian factor mutations in *Œnothera*, it would appear that this is partly due to their presence being masked by the greater number of lethal factors. And since lethal factors must produce non-viable gametes or zygotes, *i.e.*, sterility of pollen, ovules or seeds, this is in accord with the large amount of sterility in *Œnothera*. For this reason, except in the case of mutations involving visible changes in the chromosomes, we can seldom be sure in *Œnothera* that the germinal change in a locus of a chromosome which marks the origin of a mutation, did not happen several or many generations previously. It is this contingency with regard to various mutations that has made it possible to suggest that the phenomena are merely the result of the splitting out of factors acquired in some previous hypothetical cross. This argument has been used, notwithstanding the fact that mutations occur in such well-authenticated and self-pollinated species as *Œ. biennis*.

It is an interesting and significant fact that although *Drosophila*, like most animals, can only be perpetuated by a crossing of two individuals in every generation, while in such species as *Œ. biennis* natural crossing is a very rare event at best, yet the bogey of hybridization which is so often raised as a complete explanation of the mutations in *Œnothera*, has never, so far

as I am aware, been suggested for *Drosophila*. Probably the reason is that in *Drosophila* the evidence is clear that most of the mutations at any rate have had their beginning in the germ plasm at the time they make their external appearance. A great deal of ink would have been spared if it had been recognised that for plants as for animals, for *Œnothera* as for *Drosophila*, mutation is a process *sui generis*, a "spontaneous" disintegration or alteration of elements in the germ plasm which finds certain physical parallels or analogies in the behaviour of the atom of radium and other radio-active substances. To attempt to explain away mutations by assuming that nothing new has really appeared is tantamount to a denial of evolution. Zoologists are fortunate in being free from this bogey, and in being able to recognise that whatever effects crossing may sometimes have on germinal behaviour, mutations take place which have no direct reference to it.

Some of the more intricate details connected with the *Drosophila* experiments will be referred to later. We wish here merely to point out the way in which the plant and animal studies on mutation are reacting on each other for their mutual benefit. The clear-cut conception of lethal factors derived from *Drosophila* has been a great advantage in replacing the more indefinite conceptions of "sterility" in *Œnothera*. Again, the duplication of a chromosome in *Œnothera* is paralleled in several features by the non-disjunction of the sex-chromosomes which sometimes occurs in *Drosophila*.

CHAPTER III.

Forms Having an Extra Chromosome.

For a long time it was generally supposed that *Œ. lata* and forms showing similar characters were the only ones containing an extra chromosome. Fifteen chromosomes had been announced in certain other forms by Miss Lutz (1908), but without convincing evidence. Then a very different form, *Œ. incurvata*, having 15 chromosomes, was described from the Swedish *lamarckiana*,[1] and Miss Lutz (1916, 1917) has more recently published her studies, which seem to show that the occurrence of mutations with an extra chromosome is much more frequent than was formerly supposed. Hance has also (1918) found 15 chromosomes in the mutant *scintillans*. This raises problems with regard to the relationship between these forms.

It was natural to suggest that there might be seven distinct types in this series,[2] with a different chromosome of the haploid series figuring in each case. The number of types apparently with 15 chromosomes is now considerably in excess of seven, but as will be observed from Table I, some of these appear to arise only from *lata* × *lamarkiana*. This is undoubtedly a significant fact.

Now if we call the haploid series of chromosomes in *Œnothera* ABCDEFG and assume that A is the extra chromosome in *lata*, then its chromosome formula would be AAABBCCDDEE-FFGG ; and when the odd chromosome passes undivided to one pole in the reduction division without further irregularities, the gametes formed will be ABCDEFG and AABCDEFG. That is, there are three members of the A chromosome, two of which enter one gamete and one the other. It seems clear that such 15-chromosome forms as *semilata* Gates, *exilis*, *exundans* and Miss Lutz's type 5365 are derived through a secondary modification from *lata*. The evidence is strong that *semilata* Gates at any rate arises only from *lata* × *lamarckiana*. It appears very probable, on account of its characters intermediate between those of *lata* and *lamarckiana*. and also from its origin only from *lata*, that the extra chromosome is the same in both.

In order to have a *different* chromosome become the extra one in the sense in which it appears to be in *lata*, by selfing this mutant (See Table 1), we must suppose that a gamete, which is, say,

[1] The Mutation Factor, p. 147.

[2] Gates and Thomas, 1914.

TABLE I.

Mutations in *Œnothera* with an extra chromosome.

Parent Form.	Mutant.	Chromosome number.	Author.
lamarckiana, biennis, &c.	*lata*	15	Lutz, Gates, 1912. Gates & Thomas, 1914
lata × *lamarckiana* ...	*semilata*, Gates ...	15	Gates & Thomas, 1914
Swedish *lamarckiana*	*incurvata*	15	Gates, 1915a.
	lata	15	Gates & Thomas, 1914
	semilata	15	,, ,,
rubricalyx × *grandiflora*	*lata*	15	
rubricalyx	*lata* or *semilata* ...	unc't'd.	Gates, 1915a, p. 110.
biennis semigigas × *biennis*	unnamed ...	15	De Vries, 1915b.
lamk. × *biennis nanella*	*lata* hybrid ...	15	De Vries, 1915b.
lamarckiana	*scintillans* ...	15	Hance, 1918.
lamarckiana	*albida*	15	Lutz, 1908, 1917.
lamarckiana	*bipartita*	15	Lutz, 1917.
lamarckiana	modified *oblonga* (type 5509)	15	,, ,,
lata × *lamarckiana* ... *lamarckiana* ...	*nanella lata* ...	15	,, ,,
lata × *lamarckiana* ... *lamarckiana* ...	*subovata*	15	,, ,,
Nanella	dwarf type 2256	15	,, ,,
lata and *lata* × *lamk.*	type 4499 ...	15	,, ,,
lata selfed	*exilis* ... ... *exundans* ... ... type 5365 ...	15	,, ,,
lamarckiana	type 2806 ...	15	,, ,,
lamarckiana	*elliptica*	15 (?)	,, ,,
lata × *lamarckiana* ...	*rubrinervis*, de Vries	14+1	,, ,,
lata × *lamarckiana* ...	*aberrans*	14+1	,, ,,

ABBCDEFG, fertilizes one which is ABCDEFG. Such gametes could arise from an $\frac{AA}{ABB}$ meiotic separation in *lata* in the first case, and an $\frac{AB}{AAB}$ separation in the second case, the ABB and AB groups (disregarding the other chromosomes) then uniting in fertilisation to form a nucleus with 2 A's and an extra B, although derived from a plant in which there were two B's and three A's. The chances of this happening are small, especially when we remember that *lata* produces practically no functional pollen grains, and that these nearly all have 7 chromosomes. Nevertheless it is not impossible.

In *lata* × *lamarckiana* the chances of getting a mutant with a *new* extra chromosome are greater than in *lata* selfed, for we may suppose (1) that a 7-egg, *i.e.*, ABCDEFG, is fertilised by a sperm having two members of some other pair than A, the latter condition having arisen through an irregular separation involving the non-

disjunction of that pair in meiosis, *i.e.*, AB ♀ + ABB ♂, or (2) that an AAB egg (*i.e.*, having 8 chromosomes) is fertilised by a BB sperm resulting from a $\frac{BB}{AA}$ segregation in meiosis in *lamarckiana* or (3) that the segregation in the megaspore AAABB is $\frac{ABB}{AA}$, the ABB megaspore surviving and being fertilized by a sperm AB, *i.e.*, the normal type, to give an AABBB individual.

While it is thus possible for a new extra chromosome to arise in the offspring of *lata* or *lata* × *lamarckiana*, yet the chances are considerably greater that the same one will remain the extra one. The probability of such forms as *exilis* and *exundans* depending on the same extra chromosome as *lata*, depends on their frequency in the offspring of *lata*, which is at present unknown.

Returning now to the *lata*-like forms, de Vries (1909) described a form which he called *semilata*, and this arose three times independently from *lata*. One of them when selfed gave 358 offspring, of which 3 were *nanella*, 4 *lata*, and the remainder *semilata*. There is some reason[1] for believing that this form may perhaps have had 16 chromosomes. On the other hand, the writer described what afterwards proved to be a different form[2] under the name *semilata*. This stands midway between *lata* and *lamarckiana*, has 15 chromosomes and is only known to arise from *lata* × *lamarckiana*. When selfed this *semilata* gives *semilata* (15 chromosomes), *lata* (15 chromosomes) and *lamarckiana* (14 chromosomes).[3] The relation between these two 15-chromosome types is therefore a close one, and the differences between them can hardly be due to the presence of a different extra chromosome. It is conceivable, for example, that *semilata* might arise from a *lata* egg having 7 chromosomes + a *lamarckiana* male cell with 8, derived through a fresh irregular division. But this explanation would appear to apply better to other 15-chromosome *mutants*. *Semilata* appears rather like a somewhat modified *lata*, and the fact that, as shown elsewhere[3] it exhibits a series of stages running on the one hand towards *lamarckiana* and on the other towards *lata*, supports this view. We may therefore suppose it originates from an 8-egg + a 7-sperm.

Another important fact in this connection is that *Œ. scintillans*, another mutant from *Lamarckiana*, in now known (Hance 1918) to

[1] See Gates, 1915a, p. iii, footnote.

[2] l.c., p. 112.

[3] Gates and Thomas, 1914, p. 532.

have 15 chromosomes. De Vries showed (1909, Vol. I, p. 244) that this form also behaves in a peculiar way in inheritance, usually giving rise to an average of about 57% *Lamarckiana*, 32% *scintillans* 9% *oblonga* and 1% *lata*. In one family as much as 69% *scintillans* was obtained. It is significant that several of the original *scintillans* mutants were from *lata* pollinated by *Lamarckiana*. From these results it would appear that *scintillans* originates from the union of two germ cells, one carrying 8 chromosomes and the other (or perhaps the same one) carrying the *oblonga* qualities. On the other hand, it is possible that the *oblonga* type to which it gives rise, has 16 chromosomes, as Miss Lutz (1917) suggests. Also, while *lata* had a mutation frequency in de Vries' cultures of 0·413%, the frequency of *scintillans* was only 0·038%.

As predicted in 1915,[1] the cytological study of *scintillans*, resulting in the determination of an extra chromosome in its nuclei, throws much light on its origin and behaviour. It seems reasonable to interpret *scintillans* as arising from a germ cell with an extra chromosome—one bearing the *oblonga* characters—just as we picture *lata* arising from a germ cell with an extra chromosome and one having the typical *Lamarckiana* characters. This will depend, however, on the chromosome counts in the various *oblonga* types, which are at present uncertain. That the offspring of *scintillans* were always found to include 1% or more *lata*, shows a close relationship between these two types, and indicates, though it does not prove, that the extra chromosome may be the same one in both cases. Another alternative is that any chromosome, if present in duplicate in a germ cell owing to non-disjunction in the reduction division, will give the *lata* features if combined with a *Lamarckiana* germ cell or *scintillans* if combined with an *oblonga* germ cell. This is improbable for many reasons.

In regard to the relation between these forms, *lata*, *semilata*, and *scintillans*, we thus appeared at one time to be left with only two alternatives, either that the extra chromosome is the same in every case, as the breeding data suggest,[2] or that any of the 7 haploid chromosomes when duplicated will give the same morphological result. The latter alternative is highly improbable for general cytological reasons. However, while the frequency of *lata* is certainly greater in the offspring of *scintillans* than of *Lamarckiana*, it is conceivable that its unbalanced condition may lead to more frequent chromosome irregularities.

[1] The Mutation Factor, p. 142.

[2] It seems highly probable that in *lata* and *semilata* at least, the extra chromosome is the same.

The Swedish race of *Œ. lamarckiana* also yielded not only *lata* and *semilata* but also another form, having 15 chromosomes, called *incurvata.*[1] One of the latter when selfed yielded 5 *incurvata* and one like *lamarckiana.* In this case there is more probability that a different chromosome was involved as the extra one, since no *latas* appeared in the offspring of *incurvata.* But there is no certainty owing to the small numbers involved, an unfortunate result of the great amount of sterility in all these forms.

Other forms having 15 chromosomes will be considered in the discussion of parallel mutations, but it may here be pointed out that a race of *Œ. biennis* produces a *lata* mutation which is an exact parallel to the *lata* from *lamarckiana*, and which has 15 chromosomes[2]. In the *biennis* from the Holland sand dunes, known to have been naturalized there since the time of Linnaeus, Stomps (1914) obtained a *semigigas* mutant. When pollinated by de Vries (1915b) with pollen from pure *Œ. biennis* without the flowers being castrated, it produced 19 offspring,—one dwarf, 10 *biennis* with 14 chromosomes and 8 of a new unnamed type having 15 chromosomes. The latter shows no resemblance to *lata*, but from the description it appears to have several characters in common with *incurvata.* It strongly supports the evidence from *incurvata* that independent 15-chromosome types exist. Regarding its origin in 8 individuals from a cross, one must suppose that the reduction divisions in the megaspores of *Œ. biennis semigigas* produced embryo-sacs, about half of which contained eight chromosomes in their nuclei and half seven chromosomes, the remainder having been extruded or lost through irregularities in division. That such extrusion was not a haphazard and irregular phenomenon, however, is indicated by the fact that these 8 individuals all belonged to one type.

Another *lata*-like mutant was obtained by de Vries (1915b, p. 186) from *Œ. lamarckiana* × *Œ. biennis nanella.* It had in addition to the marks of *lata* the characters of the ordinary hybrid type *Œ. lamarckiana* × *biennis*, and confirms the conclusions of the writer[3] regarding the origin of *Œ. lata rubricalyx* and other *lata*-like forms in hybrids.

Finally we may consider the important studies of Miss Lutz (1916, 1917) on forms with an extra chromosome. It is to be hoped that her counts of chromosomes, which appear hitherto to have been made almost entirely from root-tips and other somatic tissues

[1] The Mutation Factor, p. 147.

[2] Gates and Thomas 1914.

[3] Gates, 1914, p. 265.

may be supplemented and confirmed by studies of the germ-cells. For, while her counts are probably correct, yet the phenomena of fragmentation of chromosomes in somatic cells make it highly desirable that they should all be checked by observations on the chromosomes during meiosis. She has determined the chromosome number in 234 plants, including sixteen different mutant types, 11 of which types had 15 chromosomes, three had 16, and two were triploid. That *Œ.* mut. *albida* has 15 chromosomes has been verified by counting the number in thirteen more plants. As will be seen from Table I, she finds an extra chromosome also in a new mutant called *bipartita*, in *subovata*, *elliptica* (?) and "type 2806," all from *lamarckiana*. In addition, a second dwarf type, unlike *nanella lata*, is found, *lata* as well as *lata* × *lamarckiana* give "type 4499" with 15 chromosomes, while *lata* self-pollinated produces *exilis*, *exundans* and "type 5365." None of these latter forms are described, so it is impossible to judge of their claims to separate status, but it seems clear that the three forms appearing in the offspring of *lata* selfed are secondary in origin, *i.e.*, bear some special relation to *lata*. All that can be said about these forms at present is that there appear to be at least seven distinct types which might arise through duplication of different chromosomes, and that in addition a number of these types appear to be more closely related to *lata*. This is certainly the case with *semilata* Gates, and probably to a different degree or in a different way with several others. This may be connected with other differential factors, but it is useless to speculate about the matter until the facts themselves are clearer. Mut. *oblonga* apparently has some forms with 15 chromosomes and some with 14. The same is true of *rubrinervis*. In this case the true *rubrinervis* of de Vries, a rather weak form, has 14 chromosomes plus a small one. The form which other investigators have called *rubrinervis*, derived from seeds of de Vries, is taller and more robust and certainly has 14 chromosomes. It is the form of my cytological studies (Gates 1908), the form from which *rubricalyx* originated (Gates 1911), and may be called *rubrinervis* Gates for identification. It is more like the *subrobusta* of de Vries, which is derived from *rubrinervis* × *lamarckiana*, and may perhaps be identical with that form or with the closely related *erythrina* (de Vries, 1919) to be discussed later.

Miss Lutz concludes that a very large percentage of the mutant offspring of *Œ. lamarckiana* have 15 chromosomes, there being both a larger number of distinct types and a higher percentage of mutant individuals with the extra chromosome. One would feel safer

about this conclusion if control counts of chromosomes had been made in the germ cells.

At least two of these reputed 15-chromosome forms, *rubrinervis* de Vries and *albida*, "breed true." Miss Lutz points out that this can only take place (1) by apogamy, of which there is practically no evidence, or (2) when two gametes having different chromosome numbers only (one odd and one even) unite to produce viable seeds. Moreover, it is possible as regards *rubrinervis* that this individual derived from *lata* × *lamarckiana* and having a small extra chromosome may differ in some respects as yet unobserved from other *rubrinervis* mutants derived from *lamarckiana* direct and possibly not having the extra fragment. More critical study of *albida* may lead to a similar result.

A number of other mutants recently described, such as *cana*, *pallescens*, *lactuca*, and *liquida* from *Œ. lamarckiana* (De Vries 1916b), which split in their offspring and are closely related to each other in several features, may contain an extra chromosome. The same may be true of *Œ. stenomeres* mut. *lasiopetala* (Bartlett 1915c). These forms will be considered later.

One of the most interesting results obtained by Miss Lutz (1916), is the existence of two types with a small extra chromosome—a fragment. In *rubrinervis* (one plant) 125 mitotic figures showed the small chromosome, and in 52 of them all the chromosomes, 14^{+1}, could be counted. The small chromosome is constantly larger than in the new type *aberrans*, of which there were two individuals. In one plant 30 figures and in the other 8 figures all showed 14^{+1} chromosomes.

In a former paper (Gates and Thomas, 1914) it was shown that a variety of irregularities occur in the meiotic divisions in pollen formation of *Œ. lata*, *semilata* and other forms which are more or less sterile in pollen. This included cases of fragmentation or pulling apart of chromosomes, particularly the odd one, on the heterotypic spindle. It might be expected that such fragments would occasionally be included in the daughter nuclei, and if they afterwards persisted they might be perpetuated by the mitotic mechanism. This is apparently what has happened in *rubrinervis* de Vries and *aberrans*, and it is significant that these three individuals all appeared in the offspring of *lata* × *lamarckiana*. The writer does not agree with Hance (1918) that they probably represent merely a temporary fragmentation of certain somatic chromosomes. Obviously if new forms can arise having gained a

small chromosome fragment, others may have lost a fragment; and this renders probable another type of germinal change, in which the redistribution of fragments of chromatin may take place. It was formerly pointed out (Gates and Thomas 1914) that all these "irregularities" will become the basis of germinal changes if they are perpetuated by mitosis. Some of the differences between 15-chromosome types may yet be explained on this basis.

This brings us to another subject closely connected with the extra chromosome, but which concerns also the question of chromosomes constancy in *Œnothera.* Hance (1918), in the paper already referred to, has studied variations in the number of somatic chromosomes in *Œ. scintillans.* The writer[1] first pointed out such variations in the somatic cells of *Œ. lata*, the number ranging from 12 to 20 or 21. Hance finds that the number of separate bodies in metaphase ranges from 15 to 21, the higher numbers being produced by transverse segmentation of certain of the chromosomes. This matter is of minor importance and will be referred to later. A fact of more interest is that more or less constant differences are found between the lengths of the different chromosome pairs in the group of 15. The pairs of chromosomes form a graded series, each somatic pair differing in length from the next longer by about 9%. This conclusion is based on careful measurements of enlarged drawings of the metaphase chromosome group in 114 somatic cells from different individuals, selected on account of their special clearness and flatness. Of these cells 51 or 45% contained 15 chromosomes, and in each case the sum of the lengths of all the chromosomes was approximately the same, showing that increase in number was due to transverse fragmentation. This demonstration of constant differences in the length of the somatic chromosomes is an important advance in our knowledge of *Œnothera* chromosomes. While differences in size have been previously observed, they have been assumed to be due merely to fluctuation, not being great enough to demonstrate except by comparison of measurements from many cells.

Hance assumes that the odd or extra chromosome in *Œ. scintillans* is the shortest of the 15. It might equally well be the longest so far as his data show. His only direct evidence is the difference in total length of the chromosomes in the two telophase groups of 7 and 8 chromosomes respectively in the heterotypic mitosis of the pollen mother cells. This difference is

[1] Gates 1912b.

2·6 units, but since the chromosomes of the germ cells are shorter and stouter than in the somatic cells this difference cannot be directly compared with the length of the odd chromosome. Hance also concludes that there is no evidence of pairing of the somatic chromosomes. In this we cannot agree, as we believe that in other *Œnothera* forms the pairing, though weak, is sufficiently indicated in certain cases so that the extra or unpaired chromosome may sometimes be directly determined by this method (see Gates and Thomas 1914, pl. 35, Figs. 5, 6, 7, 10, 11, 15). Again, we have not found that accurate drawings of the chromosomes will show them to be of uniform width with even margin throughout, as Hance's figures would indicate, although the departure from uniformity in width is not. as a rule, great.

Coming now to the question of chromosome number in somatic tissues, it would seem at first impossible to reconcile the apparently contradictory results of Hance and Miss Lutz. A critical study has been made of the process of chromosome fragmentation in somatic tissues, although only incidental references to this work have been published.[1] We believe Hance has over estimated the significance of these somatic segmentations. We observed numerous " clear areas " and constricted portions of chromosomes, but the segments were almost invariably in alignment, showing clearly which belonged to the same chromosome. Moreover, delicate linin connections are usually visible connecting the two segments. Miss Lutz (1916) has made similar observations. Constrictions or incomplete segmentations have also been studied in *Vicia Faba* by Fraser and Snell (1911) and Sakamura (1915). In nearly all such cases it is clear which portions make up a given chromosome, and so it is much more sound to treat them as a whole chromosome than to attempt to rearrange these " fragments " on a hypothetical basis from measurements. Formerly we observed no segmentation of chromosomes in prophase nuclei, but more recently the writer has observed several cases of fragmentation in prophase. Nevertheless, we are inclined to look upon the phenomenon as a temporary one, related only to the mitotic cycle, and the segmentations in the prophase of one mitosis as probably bearing no relation to those of the next to follow. The name " extra " or " supernumerary " chromosomes applied by Hance to these segments is not a suitable one, for the actual number of whole chromosomes can be determined without difficulty by observation, as Hance himself has done in *Œ. scintillans*

[1] Gates and Thomas 1914.

The determinations of chromosome numbers from root tips by Miss Lutz are therefore probably correct, although it is certainly desirable that they should be confirmed by study of the germ cells. Although Hance regards the diminutive extra chromosomes of Miss Lutz in *Œ. rubrinervis* De Vries and *Œ.* mut. *aberrans* as mere temporary fragments, yet the evidence seems to indicate that they are permanent products of a fragmented meiotic chromosome dividing by mitosis, and therefore present in every nucleus. Their constant difference in size in the two forms also supports this view.

Summing up the results regarding 15-chromosome forms of *Œnothera*, we may conclude that while several of the types have probably arisen from *lamarckiana* through having different chromosomes as the extra one, yet several others, which have appeared only in the offspring of *lata* × *lamarckiana* or of *lata* selfed, evidently have a closer relationship to *lata*, than to any other form, and *semilata* Gates at least probably has the same extra chromosome. The differences between the other forms may be accounted for partly by the presence of other factors or mutant characters in addition to the extra chromosome, and partly by fresh rearrangements of the 15 chromosomes.

The same irregular meiotic division, or non-disjunction of a pair of chromosomes, also takes place no doubt in other forms, and may be expected to lead to the appearance of occasional aberrant members in other species. Winge (1917) apparently found such a case in *Staphylea pinnata*, which has 12 pairs of chromosomes, but one haploid group with 13 was found in pollen formation. Also in *Cornus glabrata*, anaphase groups of 11 and 12 were observed. Nawaschin (1911) found in the meiotic division, in the pollen mother cells of *Tradescantia virginica* that one pair of chromosomes in the heterotype division is left near the equator, where it forms a vacuole which later becomes included in one of the daughter cells. He finds it dividing later, so that two cells of a tetrad usually receive 11 chromosomes and two 11 + this body, which is called a chromatin nucleolus or heterochromosome. But the brief account leaves many points undetermined. In the pollen formation of *Callitriche verna*, Winge (1917) has described somewhat similar conditions. The diploid number of chromosomes is 16, and in the heterotype division 7 pairs are usually distributed regularly, while the other two frequently pass to positions in line with the equatorial plate but far from the spindle, where they form nuclei.

When cell walls are formed later a hexad of pollen grains is frequently produced, four large ones containing seven chromosomes and two small containing one or two chromosomes each. It is doubtful if any of these pollen grains are functional—regular meiosis takes place occasionally—but it is interesting that a pollen grain with only one chromosome, though diminutive, can still form its exine covering in an apparently normal manner. And such irregularities always make it possible that an extra chromosome may find its way into one of the daughter nuclei, as in the origin of *Œ. lata.*

WHAT IS THE SIGNIFICANCE OF THE EFFICIENCY INDEX OF PLANT GROWTH?

By Franklin Kidd, Cyril West and G. E. Briggs.

[With Two Figures in the Text]

In a recent paper under the title of The Compound Interest Law and Plant Growth, V. H. Blackman (1) has suggested that the dry-weight of an annual plant increases at continuous compound interest, expressed mathematically by the formula $W_1 = W_0 e^{rt}$ where W_1 is the dry-weight of the plant at the end of the time t, W_0 the initial seedling or seed weight, the rate of interest and e the base of the natural logarithms.

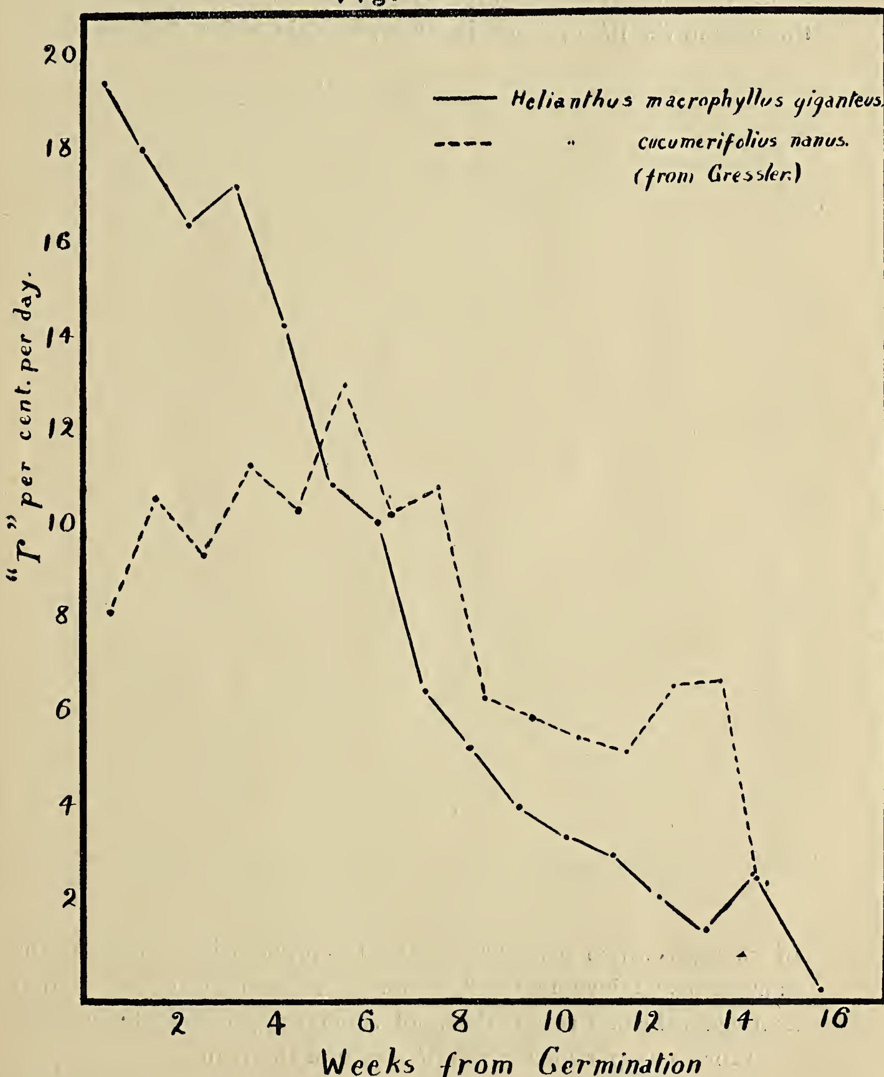
Subsequently a paper by Brenchley (2) has appeared in which the writer has applied this formula. Although the conception of plant growth as a process similar to that of money increasing at compound interest is a useful one, and indeed was put forward by two of the present writers in a previous communication (5), we think it is already clear that a more complete analysis of existing data on plant growth does not warrant so rigid an application of the conception as that made by Blackman and adopted by Brenchley.

The present writers have just carried out a detailed analysis of the carefully recorded growth data of Kreusler and his

co-workers (7) who worked with a large number of plants, and have also analysed in full Gressler's (4) data for *Helianthus*. This is now in the press (3).

In the present note we wish to point out briefly what are the implications of the compound interest formula and to indicate how

Figure 1.

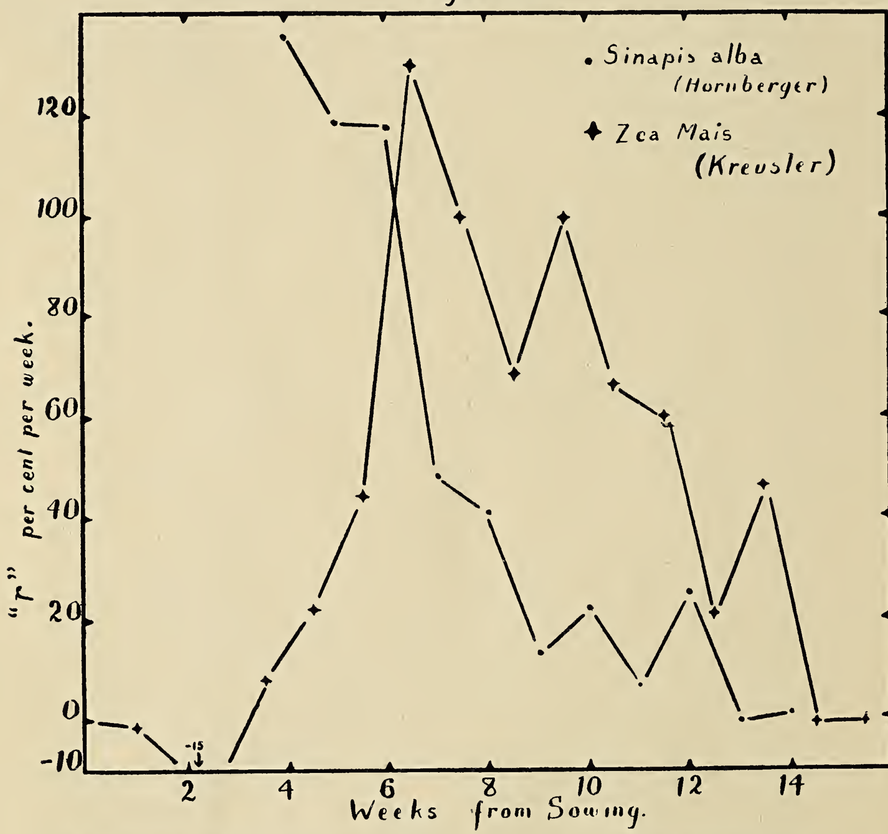


slightly these concord with the behaviour of such plants as have been so far investigated.

In figures 1 and 2 graphs for *Helianthus* (Gressler), *Zea Mais* (Kreusler) and *Sinapis alba* (Hornberger) are presented, the rate of interest from week to week being plotted against time.

If the compound interest law be applicable to the growth of a plant, the rate of interest[1] from week to week, calculated upon the assumption that the plant is working at continuous compound interest, will be constant. If this rate is plotted against time the result it will be a line parallel to the time axis. These graphs show that the rate of interest so far from being constant throughout the life-cycle of the plant, goes through a definite series

Figure 2.



of changes which are correlated with progressive stages in the morphological development[2]. Moreover the indications are that as a general rule the rate does not remain approximately constant even for short portions of the life-cycle of the plant.

[1] The rate of interest is calculated according to the following formula $\frac{\log_e W_2 - \log_e W_1}{t} = r$ W_2=Dry weight at the end of the week.

W_1=Dry weight at the beginning of the week, t=1 if the rate is weekly, 7 if daily., e is the base of the natural logarithms, and r is the rate of interest.

[2] For a more complete discussion of this question the reader is referred to (3).

It is clear that the growth of a plant obviously does not follow the compound interest law in any exact sense as implied by the equation of Blackman. It is, of course, possible to calculate the rate of interest from week to week as if the plant did follow this law, as has been done in the case of the above figures. The index r then is not a constant but a function of time or of the stage of morphological development.

Blackman says that "The rate of interest (r of the equation) is clearly a very important physiological constant. *It represents the efficiency of the plant as a producer of new material,* and gives a measure of the plant's economy in working. The rate of interest, *r*, may be termed the *efficiency index* of dry weight production. . . . . . It may also be termed the 'economy constant' of the plant; it is of course comparable to the velocity constant of a chemical reaction." The impression given by this paragraph and indeed throughout the paper is that the "efficiency index" has a physiological significance and is a constant which provides us with an important standard of comparison between plants of different species and between plants of the same species grown under different conditions.

The value of r can be determined over the whole or any part of the life-cycle. Limitations of experimental method make it impossible to observe results over short enough periods to allow the values of r to be an absolutely correct representation of actual rates, but the shorter the period the more closely do the values of r approximate to these. If a long period is taken the value of r does not represent any actual rate of increase, but merely the rate at which the plant would have had to accumulate dry material if it had increased at a constant rate of continuous compound interest throughout the period.

As indicated by Fig. 1 and as made clear by Table 1 the average value of the efficiency index for any period depends upon the period taken, and moreover in comparing one plant with another the ratio of these averages varies with the period taken. This shows that an average is not a constant for a plant nor is it a standard for comparison with other plants.

We will now consider whether the rate of interest at any point in the life-cycle calculated for the shortest possible time, gives any indication of the efficiency of the plant when comparing it with other plants for which the rate of interest is similarly calculated. The answer is in the negative, for the reason is that any

definite time the rate of interest depends not only upon the species of plant and upon the external conditions but also upon the stage of morphological development reached and upon the previous history of the plant.

The only way in which plants can be compared is by a comparison of the whole series of efficiency indices throughout their life-cycle. From such comparison useful deductions can be drawn, as the present authors have shown (3), and in a broad way the general efficiency of plants can be roughly compared.

From an economic point of view it may be suggested that r would be a useful comparison if calculated over the complete life-cycle, but here the essential idea of the "Substanzquotient" put forward by Noll and his pupils is far preferable, as it simply states the ratio of final weight to seed weight divided by time, and makes no assumption as to the rate at which the addition to dry material has been made. Unless time is of importance the ratio of final weight to seed weight is sufficient.

In order to show definitely the uselessness of r averaged over an arbitrary period or of the "Substanzquotient" for that period as a standard of comparison of the efficiency of different species we have taken the same results as those quoted partially by Blackman and have tabulated them in full (Table 1). The weights of the seedlings on germination, the weights of the plants after approximately equal periods and the efficiency indices calculated for various periods are given. The efficiency index from week to week for *Helianthus macrophyllus giganteus* and for *Helianthus cucumerifolius nanus* have also been calculated and are reproduced graphically in Fig. 1.

Column 4 shows that the average efficiency index for the first four and a half to five weeks is practically the same for four of the species but much smaller for *H. cucumerifolius nanus*; column 8 shows that the same four species after about 8 weeks still agree in having roughly the same efficiency index, and that at the same time *H. cucumerifolius nanus* is less, but whereas *H. cucumerifolius nanus* has maintained, and even slightly increased its r as compared with the first period, the other four species have all fallen off. Column 12 gives the average efficiency index up to the time of the final record of dry-weight. Whether the experiment was terminated at that point because the plants had completed their growth or whether for other reasons cannot be stated with certainty. Since the dates of the final record vary considerably,

TABLE I.

Variety of *Helianthus annuus* used.	Weight of Seedlings at Germination.	Dry-weight after 4½–5 weeks' growth.	'r'	Dry-weight for period selected by Blackman.	'r'	Dry-weight after 7½–8 weeks' growth.	'r'	Dry-weight after 12½–13 weeks' growth.	'r'	Final Dry-Weight	'r'	Final Dry-weight over Dry-weight of Seedling.
Helianthus uniflorus giganteus	0·0325 gm.	(31)* 5·868 gm.	16·8	(38)* 17·33 gm.	16·6	(52)* 46·2 gm.	14·0	(87)* 202·3 gm.	10·0	(115)* 239·1 gm.	7·75	7,357
Helianthus nanus ...	0·0347 gm.	(31) 6·15 gm.	16·7	(38) 14·80 gm.	16·0	(52) 42·2 gm.	13·7	(90) 128·7 gm.	9·1	(90) 128·7 gm.	9·1	3,710
Helianthus cucumerifolius nanus	0·00106 gm.	(34) 0·0361 gm.	10·4	(56) 0·401 gm.	10·6	(56) 0·401 gm.	10·6	(91) 3·38 gm.	8·9	(107) 6·94 gm.	8.25	6,548
Helianthus macrophyllus giganteus	0.0234 gm.	(33) 6·772 gm.	17·2	(33) 6·772 gm.	17·2	(54) 46·9 gm.	14·1	(89) 170·0 gm.	10·0	(116) 235·0 gm.	7·95	10,040
Helianthus arboreus giganteus	0·0190 gm.	(34) 4·850 gm.	16·3	(41) 14·70 gm.	16·2	(55) 45·0 gm.	14·1	(90) 134·0 gm.	9·9	(116) 285·0 gm.	8·3	15,000

* The figures in parenthesis represent the number of days' growth for which the acccompanying dry-weights are given.

the indication seems to be that the reason for terminating the experiment was completion of growth, not weather conditions. An inspection of this column will show that *H. cucumerifolius nanus*, which for all previous periods had a considerably lower average efficiency index, now has one as high as that of *H. arboreus giganteus* and actually larger than that of *H. macrophyllus giganteus* and that of *H. uniflorus giganteus*. Column 6 gives the efficiency index for the periods during which it is at a maximum and approximately constant for each species. It should be noted that the length of this period varies considerably. Finally, the last column gives the ratio of final weight to seedling weight, which after all is the value of most importance economically. A consideration of the variations in the relative values of r will show how misleading it is to state from an inspection of column 6 alone, as Blackman does, that *H. cucumerfolius nanus* has a lower efficiency and that the dwarfness of this plant is due to this lower efficiency as well as to its smaller seed. It certainly has a lower efficiency when compared with the other four species over these periods, but when compared over the whole life-cycle it has a higher economy of working than two of the other species.

Again, it is obviously misleading to compare two plants over different portions of the life-cycle for each. For example, for the period of fifty-six days *H. cucumerifolius nanus* has an average efficiency index of 10·6 whereas *H. nanus* for a period of ninety days has an average efficiency index of 9·1, thus indicating that the former has a greater economy of working: whereas comparisons for any equal period for the two plants or for the complete life-cycle show that *H. nanus* has the greater average economy of working.

Brenchley's Application of the Compound Interest Law.

In Brenchley's work two series of experiments, with mustard and barley respectively, were carried out to find the effect of competition upon plant yield. For this purpose a varying number of plants were grown per pot. The seeds were sown in double quantity and at germination were thinned out to the number per pot required. In the case of mustard (species not given) the plants were harvested after 59 days, in the case of barley after 117 days. In the case of mustard at the time of harvesting "a definite gradation of maturity occurred according to the number of plants in the pot. The single plants (per pot) were very strong, sappy, exceedingly tall and decidedly less mature than any others. . . . . In

most cases only the lowest flowers were fully developed. . . . . . The five plants per pot were of medium strength only . . . . . . and were the most mature of all. . . . . . The flowers were fully out, and many on the main stem had begun to form fruit."

In the case of the barley " the thinly seeded plants were better developed and much less mature than the more crowded specimens."

The author gives the dry-weights of the plants at the time of harvest and the efficiency indices calculated by Blackman's formula, but she does not give the seed weights.[1] As our previous discussion has shown, the average efficiency index for a given plant tends to decrease with increasing maturity, and consequently it is misleading to compare the one plant per pot which was decidedly less mature, with the other plants (other numbers per pot) which were more mature. Possibly, had the whole lot been grown to maturity—the five plants per pot would have taken less time—the average efficiency indices would have been much closer together or might have been the same.

Again, one may be tempted to compare the mustard with the barley. For this purpose the efficiency index is of no use since the plants (mustard and barley) were grown for different periods and had reached different stages of maturity.

The efficiency indices as given by Brenchley, if her seed weights were the same, are simply the logarithmic functions of the final weight divided by time, the time for each set of experiments being the same. It is quite clear that from the point of view of comparing the effect of different seedings per pot in Brenchley's particular experiments the efficiency index has no advantage over the simpler method of giving final dry-weights, assuming the seed-weights were the same, but rather the reverse, because the former implies some physiological significance of the figures given for the efficiency indices.

Summary.

A careful consideration of existing data upon plant growth does not warrant a rigid application throughout the whole life-history of a plant of the compound interest conception of plant growth advocated by V. H. Blackman and formulated in the equation $W_1=W_0e^{rt}$. The value r regarded by Blackman as a

[1] We have calculated the seed-weights from the efficiency indices and dry-weights given by Brenchley. Whereas the seed-weights in the case of barley are all exactly the same (55 mgs.), in the case of mustard (variety not stated) the seed-weights form a descending series starting from the one plant per pot (18·3 mgs.) and ending with the five seeds per pot (15·5 mgs.)

physiological constant and as an index of efficiency is not really constant at all in the plants which have been investigated. This index is of no value in comparing the efficiency of different plants, except over strictly comparable times and phases of development, so that the application of the formula by Brenchley in comparing plants of different degrees of maturity is not valid.

Botany School, Cambridge. *February, 1920.*

LITERATURE CITED.

1. Blackman, V. H. The Compound Interest Law and Plant Growth. Ann. of Bot., XXXIII, 1919, p. 353.
2. Brenchley, W. E. Some Factors in Plant Competition. Ann. of Appl. Biol., VI, 1919, p. 142.
3. Briggs, G. E., Kidd, F. and West C. Quantitative Analysis of Plant Growth. Ann. of Appl. Biol. VII, 1920. (In the Press).
4. Gressler, P. Über die Substanzquotienten von *Helianthus annuus*. Inaug. Diss., Bonn, 1907, pp. 1—25, tables I—V.
5. Hornberger, R. Untersuchungen über Gehalt und Zunahmen von *Sinapis alba* an Trockensubstanz und chemischen Bestandtheilen in 7—tägigen Vegetationsperioden. Landw. Versuchs—St., XXXI, 1885. p. 415.
6. Kidd, F. and West, C. Physiological Pre-Determination. The Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield. IV. Review of Literature. Chapter III. Ann. of Appl. Biol., V, 1919, p. 220.
7. Kreusler, U. *et al.* Beobachtungen über das Wachsthum der Maispflanze. Landw. Jahrb., 1877-9

THE SIGNIFICANCE OF THE EFFICIENCY INDEX OF PLANT GROWTH.

By V. H. Blackman.

BY the courtesy of the authors, Messrs. Kidd, West and Briggs, I have seen in typescript the paper, which appears in this number of the New Phytologist, entitled "What is the Significance of the Efficiency Index of Plant Growth?"

The main point of the paper on The Compound Interest Law and Plant Growth, which recently appeared in the *Annals of Botany* (XXXIII, 353, 1919) was to stress the view that no conception of the growth of an annual plant was satisfactory which did not take into account the fact that the capacity for dry weight production increased with time on the compound interest principle. Accordingly it was suggested that the best way of comparing the activity in dry weight production of two plants was to compare the rate at which the material already present could produce new material. On the assumption that the material was added continuously—an assumption which is, of course, only an approximation to the truth except in the case of plants grown in continuous light—a formula was put forward by which this activity, or the "efficiency index" as it was termed, could be calculated.

In their paper Kidd, West and Briggs call in question the value of the efficiency index as a measure of a plant's activity on the ground that the index is very variable. That the efficiency index is a variable quantity is, of course, obvious, for it must be markedly affected by external conditions; by light deficiency, for example, it can be reduced to zero or even to a minus quantity. Also Gressler's results, which were quoted, showed clearly that the efficiency index fell off markedly in later periods of growth.

The marked fluctuations in the index which have been demonstrated by Kidd, West and Briggs for Maize, Mustard and Sunflower, and by Brenchley for the Pea (in a paper in the forthcoming number of the *Annals of Applied Biology*, Vol. VI, No. 4), are of great value in that they provide a deeper analysis of the growth-relations of the plant at various stages. These fluctuations in the efficiency of the plant do not, however, affect the value of the efficiency index, for it is obvious, and it is indeed clearly stated in the original paper (pp. 357 and 358), that all that the calculation gives is the *average* efficiency index. Kidd, West and Briggs state that the efficiency index if a long period is taken "does not represent any actual rate of interest, but merely the rate at which the plant would have had to accumulate dry material if it had increased at a

constant rate of continuous compound interest." This is of course perfectly true and state the nature of the index very clearly. The efficiency-index-like averages in general is only an abstraction, but it is none the less valuable as a basis for comparison.

The three authors further insist that the *only* way in which plants can be compared is by a comparison of the whole series of efficiency indices throughout their life-cycle. This is rather a large claim. Surely in the absence of such full data the comparison of the average efficiency for larger periods or for the whole life-cycle is of value. And even if the daily or weekly efficiency indices are available for the whole life-cycle it is still useful for purposes of comparison to sum up the activity of the plant for longer periods by calculating the average efficiency index on the supposition that it is constant throughout those periods.

The efficiency index was described as an "important physiological constant." The word "constant" might have been put in inverted commas in the original paper, for the only real constants of a living organism are, no doubt, those of the physical and chemical processes of metabolism. There is, however, a precedent for the use of the term for the rate of an important physiological process, for Dugger, in his book "Plant Physiology" (p. 255), uses the term for the average rates of such physiological processes as photosynthesis, transpiration, etc. It should have been clear that the use of this term "constant" in relation to the efficiency index did not, and could not, imply that the rate of addition of new material was an invariable quantity.

In supposing that the index would be the more accurately determined the shorter the period of time under consideration, the three authors are pressing too closely the analogy with a physical constant, and exhibit a failure to realise—and this seems to lie at the basis of their criticism—that the index is almost necessarily only an average of a number of widely differing rates.

Data obtained from daily periods would not necessarily be any more valuable than those for longer periods, nor hourly data any more valuable than daily ones. A little consideration will show that, except for plants grown under external conditions which are kept artificially constant, the rate of increase of material must wax and wane with the rising and setting of the sun, and that during the night the rate becomes a negative quantity. The efficiency index when applied to plants growing under natural conditions is thus necessarily only an average or conventional measure of the plant's

activity in the production of new material.[1] It is clear that owing to the marked fluctuation of the index over even such a short period as 24 hours some such convention is essential if we are to compare the activity of different plants.

It has further been suggested in criticism that "the essential idea of the 'Substanzquotient' put forward by Noll and his pupils is far preferable, as it simply states the ratio of final weight to seed weight divided by time, and makes no assumption as to the rate at which the addition to dry material has been made." In relation to this criticism it must be pointed out at once that the last statement cannot be accepted. A formula in which the final weight is divided by seed weight and by time implies that there is a linear relation between time and weight (*i.e.*, that the increase of weight is an arithmetical progression) just as definitely as does the formula I put forward carry the implication that the relation between time and weight is a logarithmic one (*i.e.*, that the increase of weight is of the nature of a geometrical progression). A simple formula is no less based on theory than a more elaborate one.

The question as to which formula is the more suitable is simply the question as to which hypothesis most closely fits the facts. That plants do to a large extent add new material on the compound interest principle can hardly be denied. It would seem also that annual plants when growing under favourable conditions add the main mass of their material at a rate which constantly increases with time (see for example, Fig. 4 of Dr. Brenchley's in the forthcoming paper already cited). A formula which takes this mode of increase into account by assuming an average or conventional index, would seem then more satisfactory as a comparative measure of efficiency than one which implies the addition of new material at a constant rate.[2]

The authors have also criticised the exhibition in the original paper of the data from Gressler's work on *Helianthus*. The times chosen for the various species were those for which it appeared that the geometrical increase of dry weight was most marked. They served to bring out the marked difference in the economic rate at which these plants were working *during these periods*. The

[1] The use of the term "constant" can on this ground be defended as *literally* correct, since for any given experiment and any given period the index is an absolute constant, albeit a hypothetical one.

[2] It may be that to some plants growing under unfavourable conditions, or with a long period of slow growth in the latter part of their development, the simple "arithmetical" formula would more aptly apply. Even in these cases, however, for purposes of comparison with other plants the compound interest formula may conveniently be used.

fluctuations in the efficiency index, on which the three authors rightly lay stress, clearly indicates that caution must be exercised in making deductions as to a plant's *general* economy of working from the efficiency index calculated over short periods, but the efficiency index does nevertheless give a measure of the plant's *average* efficiency *during any particular period.*

As was pointed out in the original paper we know nothing of the experimental errors of Gressler's results and he admits that the number of plants used for the dry weight determinations was sometimes very small so that the results cannot with assurance be subjected to a very close analysis. Up to the 7½-8th week the dwarfness of *H. cucumerifolius nanus* is certainly due to a low efficiency index as well as to a small seed weight, as the table provided by Kidd, West and Briggs shows, for the index of this plant is markedly lower than that of any of the other four forms; and even up to the 12½—13th week the index of this particular species is still the lowest. It is true that when the last determination is made the indices of both *H. uniflorus giganteus* and *H. macrophyllus giganteus* fall below that of *H. cucumerifolius nanus.* It is to be noted, however, that during the last period of growth shown in the table the dwarf form more than doubles in weight, while the two other forms increase only 18% and 38% respectively, in spite of the fact that the period in question is longer. It is obvious that the average efficiency index over the whole period of growth has been reduced, both in the case of *H. uniflorus* and *H. macrophyllus*, by a long period of slow growth in the last stage of development. Whether this period is absent in *H. cucumerifolius nanus* or the plants were cut down too early to exhibit it is not clear; the latter would seem more probable.

The three authors have also criticised Dr. Brenchley's use of the efficiency index in exhibiting some of her results. In the case of the barley plants she investigated the plants differed in maturity in relation to harvesting, but it is clear that they had practically reached their full size, and in Dr. Brenchley's opinion it is probable that in all of them increase of dry weight had ceased. The mustard plants if allowed to continue growth would certainly have increased considerably in dry weight, but as already stated the efficiency indices do give a measure of the economy of working of the various sets under the given conditions and for the given period, and so exhibit the effect of external conditions more accurately than do the final dry weights alone.

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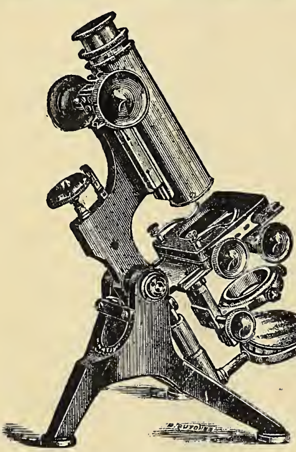

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PHYSIOLOGICAL ANATOMY OF XEROPHYTIC SELAGINELLAS.

BY J. C. TH. UPHOF, PH.D.

[WITH TEXT-FIGURES, I-XII.]

THE writer has made an attempt to obtain data on the behaviour of xerophytic Selaginellas, by investigations carried out in the deserts of Southern Arizona, California, Northern Sonora, Mexico, and on bare mountain tracts and rock outcrops in eastern and south-eastern Missouri. The laboratory work was conducted at the University of Arizona, and at the Herbarium and Jodrell Laboratory at the Royal Gardens, Kew. The author is much indebted for kind help to Sir David Prain, Director, and Dr. Arthur W. Hill, Assistant Director of Kew Gardens, to Dr. Otto Stapf, Curator of the Herbarium at Kew, to Mr. L. A. Boodle, Curator of the Jodrell Laboratory, to Mr. A. Gepp, Curator of the Cryptogamic Herbarium of the British Museum of Natural History, South Kensington, and to Mr. W. Emary for preparing the manuscript for publication.

The genus *Selaginella* consisted in 1887 according to Baker (1) of 334 different species, in 1900 (*vide* Hieronymus (7) in Engler and Prantl, *Die Natürlichen Pflanzenfamilien*) of 559, and in 1910 (*vide* the present writer's (26) *Die Pflanzengattungen*) of 580 known species. Like the ferns, most species are adapted to moist, shady situations; the forests of the tropics and sub-tropics being unusually rich in various forms. About 6 per cent of the species, however, inhabit dry localities, such as deserts and rocks of the Old and New World. I found their geographical distribution closely associated with that of xerophytic ferns, as has been outlined by Christ (3), their main distribution being the semi-arid regions of Mexico, the South Western part of the United States (especially Texas, New Mexico, Arizona and California), South America, Arabia, South Africa, the Mediterranean and the deserts

of Asia and Australia. As outstanding localities may be considered rocky and sandy situations in the midst of a non-xerophytic flora; such as dry ridges and rock outcrops occurring near mesophytic forests, and sand barrens which may occur anywhere.

Although excellent work has been published on the anatomy and morphology of *Selaginella*, especially by Cornaille (4), Gibson (9, 10), Haberlandt (12), Mitchell (17), Seyd (21), and Treub (24), only Leclerc du Sablon (14) in 1889 and Wojinorvić (29) in 1890 have contributed toward the knowledge of the xerophytic *S. lepidophylla*, Spring. Since that time, very little has been done on the subject, and other xerophytic species have scarcely been studied from an anatomical and physiological standpoint; comparative studies with plants of the same species under different environment have never been undertaken, neither has a physiological-anatomical classification of the plants in question been made.

Comparing various species of xerophytic and hygrophytic Selaginellas one soon notices the very close proximity of the dorsal and ventral leaves in the former (Fig. I, 1, 4, 5, 6), and the distance between the succeeding leaves in most species of the latter (Fig. I, 3). Moreover there is a striking similarity in the size of leaves in all xerophytic species the author has worked with; the size of the dorsal leaves differs only very little from that of the ventral leaves, although they may have slightly different shapes (Fig. II, 1, 2, X, 1, 2). In all hygrophytic Selaginellas, on the other hand, the difference in size and shape of dorsal and ventral leaves is very marked (Fig. I, 3). The writer considers the similarity in size in leaves of the xerophytic species (Fig. I, 1, 4, 5, 6; II, 1, 2, 8, 9; X, 1, 2) to be of much importance from a photosynthetic standpoint, as will be shown later: under the influence of their extreme environment the ventral leaves contain but few chloroplasts. Most of the production of organic matter therefore, as far as the action of the light is concerned, has to take place in the green cells of the dorsal leaves; were these leaves several times smaller, as is the case with hygrophytic ones, an insufficient amount of organic food would be formed, threatening perhaps the existence of the species. It is suggested that this factor must have been effective at the time, hundreds of centuries ago, when xerophytic species of the type *S. lepidophylla*, originated from distinct heterophyllous hygrophytic or semi-hygrophytic forms; those adapted to arid or semi-arid situations being alone able to survive.

FIG. I. *Xerophytic species.* 1, *Selaginella pilifera* Mexican desert ; 2, from shady and moisty greenhouse ; 4, *S. Pringlei* from Mexican desert ; 5, *S. rupincola* from Arizona desert : 6, *S. sanguinolenta* from Karrum Valley Afghanistan. *Hygrophytic species* ; 3, *S. Galeottei* from shady and moist greenhouse.

Note similarity in size of leaves of xerophytic forms, and difference in size of dorsal and ventral leaves of the hygrophytic one.

One is able to arrange various xerophytic species, collected in different dry countries in three distinct physiological groups, as follows.

Group I. Plants with vertical leaves, all of the same size and shape. The apex of each leaf ends in a long awn containing no chloroplasts. The anatomical construction of stem and leaves is decidedly sclerotic. Species belonging to this group all belong to the sub-genus *Homœophyllum*, e.g., *S. rupestris*, (L.) Spring, growing in rocky places of the northern and southern temperate zone of the Old and New World; *S. rupincola*, Underw. on rocks in south-western United States and Mexico; *S. Watsoni*, Underw. from the mountains of Utah and California; *S. Bigelowii* Underw. reported from California; *S. extensa*, Underw. collected from Las Candas, Luis Potosi, Mexico; *S. Underwoodii* Hieron. from New Mexico; *S. densa* Rydl. from various parts of the Rocky Mountain States; *S. mutica*, D. C. Eaton, on cliffs in mountains of Colorado, Arizona and New Mexico; *S. Ridellii* van Es. from central and eastern Texas and probably also in southern Louisiana; *S. humifusa*, van Es. growing on dry sandy soils in central and south Florida; *S. funiformis*, van Es. from the sand dunes and barrens of Florida; *S. tortipila*, A. Br. from South Carolina, growing on granite rocks in the mountains; *S. Sherwoodii*, Underw. growing on rocky places in North Carolina; *S. acanthonota*, Underw. growing on sand barrens in Florida, Georgia and North Carolina; *S. arenicola*, Underw. on dry sandy ground and rock waste of central and north Georgia and Florida; *S. caffrorum*, Hieron. and *S. capensis*, Hieron. reported from dry places in South Africa; *S. Mildei*, Hieron. from similar places in the province San Luis, Argentine; *S. Sellowii*, Hieron. from S. Diego, Brazil. There are further some other species belonging to this group, most of them being segregated from *S. rupestris*, of which many have been described by Hieronymus, Underwood (26), and Van Eseltine (8).

Group II. Plants having slender, wiry, trailing stems, spreading over the ground, or hanging down from rocks or sometimes from trees; the foliage consisting of two rows of dorsal and two rows of ventral leaves; the size of leaves being very much alike, although the shape may differ. Leaves of some species fold themselves round the stem when dry; certain forms have a slight resemblance to the last group; e.g., *S. sanguinolenta*, Spring from

rocky situations in Afghanistan and Eastern Siberia; *S. mongholica*, Rupr. from North China; *S. borealis*, Spring from Eastern Siberia, Kamschatka and Eastern Himalaya; *S. saccharata*, A. Br. from rocky, exposed situations in Mexico.

Group III. Plants having a spreading habit, stems often forming a flat, dense and close rosette; rolling into a nest-ball during drought. To this group belong *S. pilifera*, A. Br. growing in dry, rocky places in Texas, Southern Arizona and various parts of Mexico; *S. lepidophylla*, A. Br. from similar localities in Texas, New Mexico, Southern California, and from Mexico to Peru; *S. Pringlei*, Baker, from similar places in Texas and Mexico; *S. convoluta*, Spring growing in exposed places in tropical America from Mexico to Southern Brazil; *S. longispicata*, Underw. being reported from Yucatan, Mexico; *S. cuspidata*, Link. from Cuba, Mexico, Guatemala, and Venezuela; *S. imbricata*, Spring in semi-arid localities in Arabia, Abyssinia and Zambesiland; *S. involvens*, Spring from similar places in China, Japan, Amurland, Corea, and Eastern Himalayas.

Group I.

I was able to study *S. rupincola*, in its natural state in various parts of Southern Arizona (Sabino Cañon, Aqua Caliente and Oracle near Tucson) and *S. rupestris*, in Southern Arizona (Sabino Cañon, near Tucson) Southern California (San Bernardino Mountains) and various parts of the Ozark Mountains in South Eastern Missouri. Both species are petrophilous, growing mainly on exposed cliffs and rock outcrops. Individual plants on northern and north eastern exposures are well developed, their stems and leaves being greyish green and containing living protoplasm during the entire year. The few individuals on hot southern and south-western exposures are as a rule poorly developed; during the hot spells in summer the stems and leaves are entirely yellow or yellow brown, the protoplasm being killed. It is only during the rainy season that young shoots appear, which moreover never attain the same development as those on plants growing in favourable shady situations. Of both species the stems are densely tufted, ascending or decumbent; the leaves stand vertically close to the stem. They are all alike, sessile and possessing a groove in the midrib on the dorsal side; the margins bear one-celled bristles; the apex ends in a long awn and the sporophylls form terminal, somewhat four-angled spikes. The first thing one observes about *S. rupincola* is the vertical direction of the leaves, which are

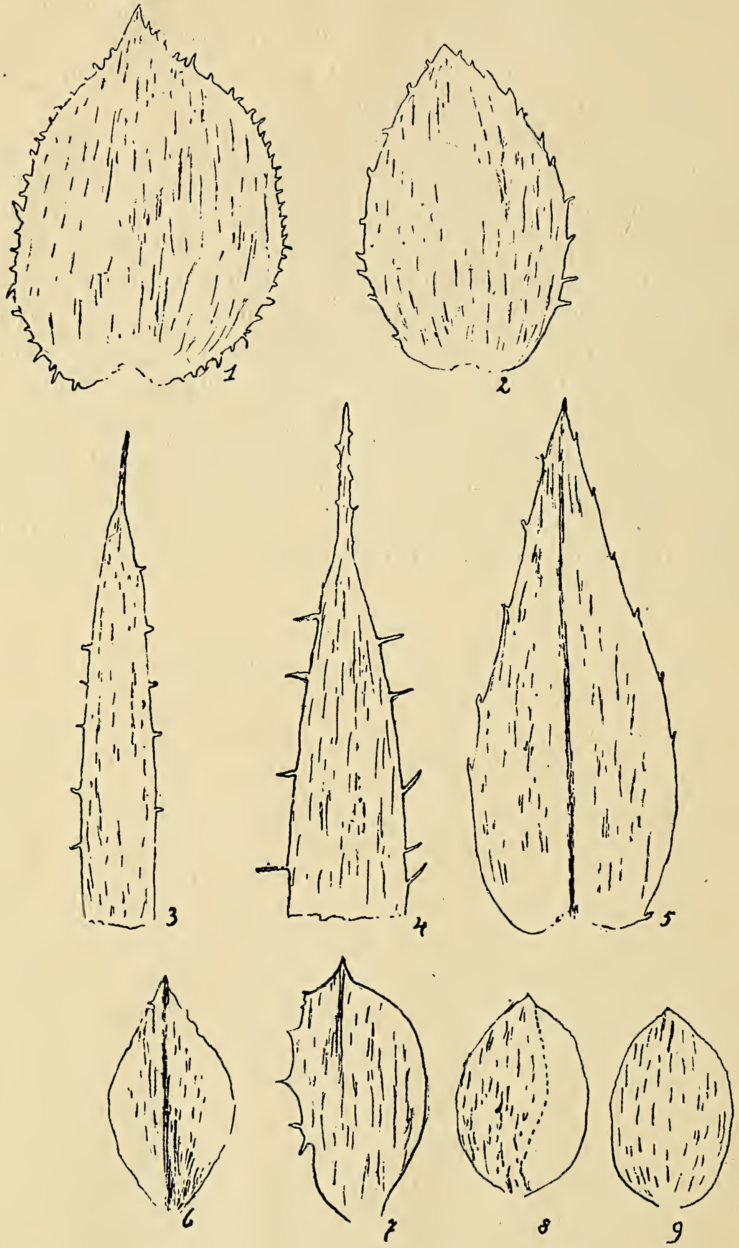


FIG. II. 1, 2, ventral and dorsal leaf of *Selaginella pilifera*; 3, *S. rupincola*; 4, *S. arenicola*; 5, *S. densa*; 6, *S. sanguinolenta*; 7, *S. borealis*; 8, 9, ventral and dorsal leaf of *S. saccharata*.

practically parallel with the stem. Only during the very hot summer when the temperature rises as high as $41\cdot5^{\circ}$ in the sun and 30° in the shade, can one recognise the advantage of this feature, when during the hottest hours of the day the sun's rays fall parallel with the leaves, whereas if the leaves stood horizontally they would be exposed to the perpendicular incidence of the rays. Further, one observes that the greyish-blue cuticle of the epidermis reflects the light to a certain extent, although this feature is not so marked as in the species of Group III. The growing point is protected by a close bundle of long awns on the young leaves surrounding the apex of the stem. The cells of these awns are elongated, thick-walled and entirely destitute of chlorophyll, reflecting almost all the light falling upon them (Fig. I, 5 ; II, 3, 4, 5 ; III, 9 ; V, 5). The same feature can be observed in all the species belonging to this group. Awns on leaves of older and lower parts of the stem do not seem to be of great importance, as a protection from the sun, but they retain the power of reflecting light. In *S. densa* the leaves are broader than those of other species (Fig. II, 5), and are folded length-wise round the stem, the halves being almost at right angles to each other, and lying very close against the stem. This structure and position of the leaves minimises transpiration. *S. densa* was collected in a dry pine wood in Dappatah, al
Florida. The same conditions exist in psammophilous species, *i.e.*, those found in sandy soils, which are for a large part of the year physically dry, on account of the rapid drainage of water after rains. Species from such localities are *S. arenicola*, *S. funiformis*, *S. acanthonota* and others.

Sections of various parts of plants of this group exhibit a very sclerotic anatomical structure. A section of the stem (Fig. III, 6), of *S. rupestris*, collected on an exposed granite rock near Sabino Cañon, shows a very thick cuticle; the cell cavities of the epidermis being very small, on account of the secondary layers of the walls. The hypodermis is usually composed of three rows of cells of the same size as those of the epidermis. The cells of the cortex are larger, and the walls become gradually thinner as one proceeds further into the plant, although they are never as thin as those of hygrophytic forms. In thin sections one readily finds in the thick walls layers and remains of plasmodesmi. The protoplasm of the epidermis, hypodermis and outer cortical cells very soon dies, after the secondary wall layers are formed. In very young tissues these cells sometimes contain a few chloroplasts,

especially the future thick-walled outer cortex, at a later age only the thin-walled inner cortex contains living protoplasm with a few chloroplasts. At first, when very young, these cortical cells contain small intercellular spaces, but these soon disappear. The vascular bundle, which is in all species simple, contains a well developed phloem; the cells of the pericycle are relatively large, the cells of the protophloem, sieve tubes and phloem parenchyma are smaller. The vessels of the protoxylem and metaxylem are considerably narrower than those of the hygrophytic forms, owing to the reduced water supply of the plants.

The cross section of a leaf (Fig. III, 7, V, 1, 7), is somewhat boat-shaped, the epidermis is thick-walled, covered by a thick cuticle. The wings of the leaf contain a thick sclerotic tissue, composed of two, sometimes of four, layers. The mesophyll is everywhere surrounded by the thick cells mentioned above; the air-spaces between the cells are small, except where stomata occur in the groove along the midrib of the aligular surface, and here the air-spaces become much larger. The stomata are protected by a very thick cuticle (Fig. III, 3), which contains opposite the entrance of each stomata, a small air chamber, leading through a narrower passage to the guard cells.

The contrast in development of tissues between plants from very dry and exposed situations, and individuals of the same species from a moist and shaded greenhouse at Kew is striking (Fig. III, 1-10). The adaptation of such xerophytic forms to a pure hygrophytic environment manifests itself at once. Plants from the latter possess almost horizontally placed leaves, instead of vertical ones (Fig. III, 5, 10). The leaf surface does not reflect the light: the awn at the apex of the leaf is considerably shorter in comparison with that of the desert type (Fig. III, 4, 9); it has entirely lost its purpose, although it is composed of sclerotic elongated cells. The sporophylls, which form a four-sided spike, lie closer against the axis of plants from dry environments, protecting the mega-and microsporangia, than is the case with the sporophylls developed in a moist environment.

A cross section of the stem (Fig. III), of the same age, shows a thinner cuticle; the cell cavities of the epidermis and of the hypodermis are larger, because the cell-walls are thinner. All the walls of the cortex are considerably thinner, and the cortical cells possess living protoplasm with 4 to 5 chloroplasts. An important feature of the vascular bundle is the greater width of the vessels in

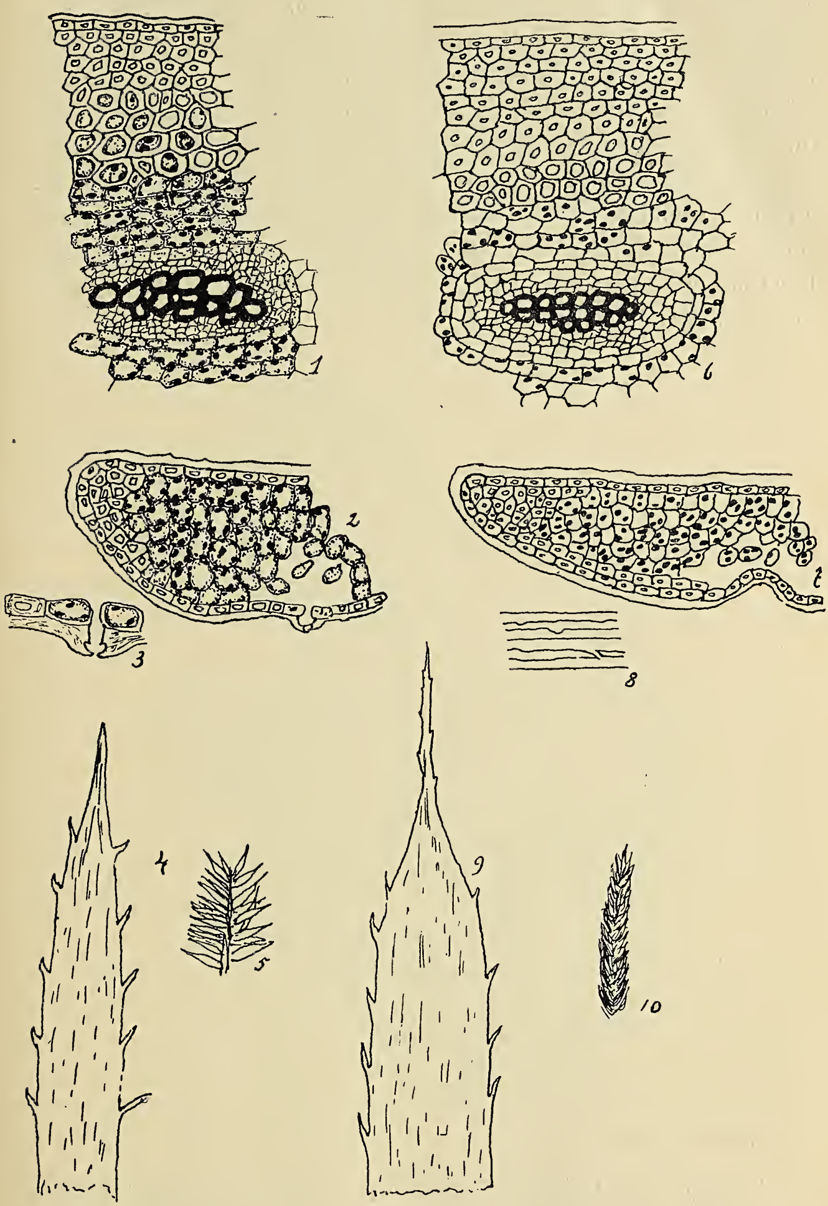


FIG. III. *Selaginella rupestris.* 1, section of stem; 2, section of leaf; 3, stomata; 4, leaf; 5, habit of plant. All developed in shady and moist greenhouse; 6, section of stem; 7, section of leaf; 8, sclerenchyma of leaf; 9, leaf; 10, habit of plant. All developed in semi-arid desert.

the xylem, because the water supply has increased; although they are never as wide as those of hygrophytic Selaginellas. The difference in size of the elements of the phloem is not considerably marked. A section of the leaf (Fig. III, 2), shows a somewhat thinner cuticle; the stomata, which also only appear in the groove on the aligular face, are present in larger number, their guard cells are covered by a thinner cuticle; although the external air chamber remains. The sclerotic cells are not as numerous, and not as thick. The cells of the mesophyll are slightly larger and have broader air spaces between them; those toward the stomata are considerably larger.

Fig. IV. Selaginella arenicola, section of stem.

Treatment with KOH shows that all the thick-walled tissues are heavily suberized in those plants grown in exposed places. The yellow color is not as intense in tissues of plants grown in the moist environment of the greenhouse, which suggests a less amount of suberine in the secondary walls. The awns and the wings of the leaves, composed of sclerotic cells, are suberised.

Selaginella arenicola, a psammophilous species, collected from a dry, sandy pinewood near Dappatah, Florida, shows a similar anatomical construction, the hypodermis, however, is thicker along certain radii of the stem, giving an irregular star-shaped form on a cross section (Fig. IV), on the other hand the stem of *S. rupestris* has a square, sometimes a five-angled shape. Old cell walls which were very exposed are impregnated with a red-brown pigment, which, no doubt, serves as a protection against very intense light. The vascular bundle of the stem shows the same characteristics as in *S. rupestris*, *S. rupincola* and *S. densa*. A cross section of the leaf shows a far more developed sclerenchyma than in the species previously described (Fig. V, 1). The stomata, which also appear on the aligular surface, are protected by stiff one-celled hairs. On a longitudinal section of the leaf (Fig. V, 6), one notices the thick-walled elongated cells of the sclerenchyma. The mesophyll contains larger inter-cellular species than in the species previously described; it is composed of roundish cells toward the upper surface, lower down they are elongated.

A section of the leaf of *S. rupincola* (Fig. V, 7) is of much the same structure as *S. rupestris*. The vascular bundles in the leaves of all species mentioned under Group I, are best developed near the base and occupy only a small portion of the centre of the leaf. The bundles are usually composed of four narrow tracheids, which are narrower than those of plants developed in a moist situation. Around the xylem are some parenchyma cells and a few sieve tubes, which do not show any differences in plants grown in various environments.

Group II.

Plants belonging to this group have a flat, spreading habit and have slender stems which are as a rule widely branched, and wholly or partly covered with small, sometimes scale-like, leaves. Some species show resemblances to the third group, as they are able to roll up during drought, but do not form a nest-ball, since they are too widely branched. One of the principal representatives is *S. sanguinolenta*. The plant examined was collected in a rocky mountainous situation in Kurram Valley, Afghanistan. The stem is very thin, spreading and pinnately branched; and the branches frequently sub-divided again; these divisions are short and covered with very small scale-like leaves (Fig. I, 6) all of the same size and shape. This species is supposed to stand near the borderline of the heterophyllous and homophyllous Selaginellas. These leaves are

convex on the aligular surface, consequently the ligular surface is concave and partly surrounds the stem; their shape is oblong, obtuse, about 0·7 to 1 mm. long (Fig. II, 6). Old parts of the stem are leafless, and possess a bright red color. There is a very thick cuticle, the cells of the epidermis, hypodermis and outer cortex, which are very thick-walled, do not show difference in size (Fig VI, 1). The inner cells of the cortex are thinner walled, retain their protoplasm longer and possess 4 to (sometimes) 6 chloroplasts. I was unable to find intercellular spaces, excepting in a few cases in very young tissues. With age the space in the thick walled cells

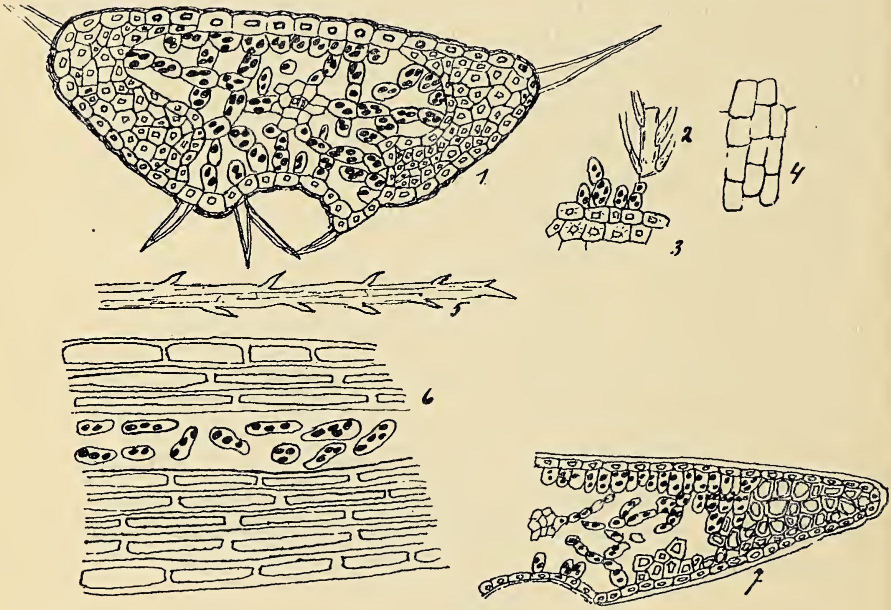


FIG. V. *Selaginella arenicola.* 1, section of leaf; 2, attachment of leaves to the stem; 3, base of leaf and part of stem; 4, part of epidermis of stem: 5, awn at apex of leaf; 6, longitudinal section of wing of leaf *rupincola*; 7, cross section of leaf.

becomes very small, through formation of secondary wall layers; all the walls are impregnated with a red or brown-red pigment, which serves as protection against intense sun's rays. Toward the vascular bundle, there is a wide sharply defined lacuna and the trabeculæ consist of narrow cells, which later sometimes divide into two. The spaces in this tissue are large, while they are absent in the plants of Group I. The elements of the meta- and protoxylem are narrower than in any xerophytic species the writer has worked with and stand in close relation with the low water requirements and supply of the small leaves. The different parts of the phloem are

all present, the cells of the one layered pericycle are relatively larger.

The leaves show on cross section a very thick cuticle, and thick epidermis cells; no sclerenchymatous tissue is developed. The mesophyll shows rather a hygrophytic character; it is composed of one layer of palisade cells, and a strongly developed spongy parenchyma, with large air spaces throughout the entire tissue (Fig. VI, 3). The stomata, which occur on both aligular and ligular surfaces, are small, and protected by a very thick layer of cuticle. The wings of the leaves are composed of thick-walled mesophyll cells which are formed close to each other, and apparently do not possess intercellular spaces.

The other species studied was *S. saccharata*, collected on bluffs near Guadalajara, Mexico. Its stems are trailing and pinnately branched. There is but little difference in the size of the leaves (Fig. II, 8, 9), which are 0·75 to 1 mm. long, the dorsal leaves of some individual plants are slightly shorter than the ventral leaves, and are pale green. The leaves of the lower plane are white when dry, reflecting the light to a considerable extent. When growing exposed to intense sun they become brown or red brown, the pigment occurring only in the cell walls, especially in the lower epidermis. During drought the younger parts of the stems curl up to such an extent that parts of the lower surface of the stem and leaves lie in the same direction as the upper surface, thus covering and protecting the true upper side of the plant against drought, heat and extreme light.

A cross section of the stem shows a thick-walled epidermis, its cuticle being especially strongly developed. The thick-walled cells of the hypodermis differ but slightly from those of the epidermis; the cells of the cortex are larger and thin toward the vascular bundle. There is a striking difference in thickness between the cortex cell walls of the uppermost part of each branch and that of the lower surface; in the former they are thin-walled, in the latter thick-walled. The difference stands in close relation to the curling movement of the branches when the plant becomes dry: this will be fully considered and explained in dealing with the species of Group III. All the cells of the cortex contain in their youth chloroplasts and air-spaces, but these disappear in the thick-walled tissues of the outer cortex. The tracheids of the xylem are narrow.

The leaves (Fig. VI, 4, 5), possess a thick-walled epidermis; the mesophyll is composed of a one celled layer of palisade parenchyma; the cells of the sponge parenchyma have the same shape as those of the palisade; the intercellular spaces are small, though distinct.

The writer regrets he was unable to study any of the plants of this group under natural conditions. The habitats of these plants, which differ widely from those of the other two groups, must have an effect on their development and behaviour, and these facts can only be satisfactorily studied in their native environment.

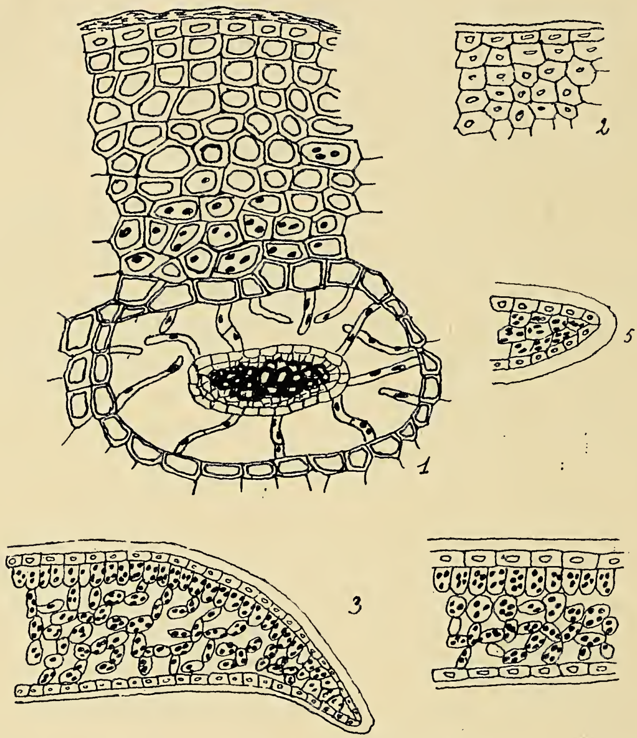


Fig. VI. *Selaginella sanguinolenta.* 1, section of leafy stem; 2, section of old leafless stem; 3, section of leaf. *Selaginella saccharata*; 4, 5, sections of leaf.

Group III.

Plants of the last group are exceedingly well fitted for a semi-arid environment. The stems are densely tufted, and curl up into a more or less close cluster; the leaves are situated horizontally on both sides of the stem; the dorsal leaves are only a little smaller than the ventral ones. The under sides of the ventral leaves, which become the outside of the cluster when curled up during drought, reflect much of the light they receive. The cells contain a large amount of oil. They form the series *Rosulatæ* of Baker (1).

The writer was able to study plants in their natural state, especially *S. lepidophylla* in Southern California (environs of San Diego), and Northern Sonora, Mexico (a few miles from Los Nogales); *S. pilifera* also was studied near Los Nogales.

Both species prefer exposed, rocky situations, especially with a northern aspect. In the neighbouring flat rockless deserts they are never met with. The plants are subject to extreme drought and intense heat; for a large part of the year under such circumstances they are to be found curled up into a big loose cluster-ball; the underside of the plant, which is alone exposed, differs in color in proportion to the amount of its exposure to the full severity of the sun. When not so exposed, owing to protection by the shadow of big rocks, this underside is almost white; the stronger the effect of the rays on the plants, the more the underside of the leaves will contain a brown to red-brown color. When illuminated by the sun's rays, the clusters appear to be more or less glossy on account of the light being reflected by the white or brownish cells. The clusters are sometimes detected with difficulty at small distances on account of the similar color of surrounding rocks and are thus easily overlooked.

The air temperature, the rainfall and relative humidity to which the species of this group are especially subject are of much importance. It is therefore necessary to give meteorological data, partly collected by the writer in the neighbourhood of Tucson, Arizona, which is under much the same weather conditions as the neighbourhood of Los Nogales, Mexico.

Air Temperature, 5 c.m. above the ground at Tucson, Arizona—
Altitude 723 metres,

Month.	Temp. in Sun °C.	Temp. in Shade °C.	Month.	Temp. in Sun °C.	Temp. in Shade °C.
January ...	18·5	12·5	June ...	35·0	25·0
February ...	24·7	15·0	July ...	38·2	26·1
April ...	30·2	20·1	August ...	41·5	30·2
May	27·3	22·0	September ...	39·0	25·5

The annual rainfall in different sections of Southern Arizona, varies with the altitude, as may be seen from the following figures; the rainy season at lower elevations is in winter.

Name of Place.	Elevation in Metres.	Summer rain in Millimetres.	Winter rain in Millimetres.	Annual rainfall in Millimetres.
Yuma ...	45	10	51	78
Maricopa ...	351	45	78	143
Casa Grande	711	40	71	130
Tucson ...	723	134	114	274
Oracle ...	1440	182	215	449

The relative humidity differs greatly, not only with the time of year, but also at different parts of the day. On very hot days at about 2 p.m. it ranges from 25 to 35, between 5 and 6 a.m. from 80 to 90, at 10 p.m. from 35 to 50. The number of cloudless days during the year is considerable, amounting to over 320.

Meteorological conditions of semi-arid regions in the Old World are similar to those in Southern Arizona. As the xerophytic plants which the author has studied are also to be found in dry regions of Asia and Africa, it is useful to give data relating to these parts of the world as far as could be obtained. Most of the data were obtained from the *Meteorologische Zeitschrift.*

Temperature, Relative Humidity and Rainfall of various Deserts.

Month.	North Africa and South West Asia.			Algerian Sahara.			West Central China.			South African Desert.		
	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.
Jan.	24·8	81·5	44·8	20·7	48	19	10·5	82	18	21·7	90	1·1
Feb.	29·8	86·0	19·0	23·8	31	7	14·0	57	0	23·9	92	1·6
Mar.	20·2	83·0	8·1	30·7	26	15	24·5	65	23	29·4	92	3·2
April	20·1	83·0	7·1	34·3	21	8	33·7	40	13	34·4	84	5·0
May	20·2	92·0	0	39·0	17	17	35·7	25	13	33·3	90	14·5
June	22·9	91·0	0	45·1	14	1	38·2	19	0	28·3	86	7·9
July	22·3	93·0	0	47·4	12	0	40·5	29	5	25·6	88	5·2
Aug.	26·7	94·0	0	46·6	15	2	35·5	30	6	26·1	87	6·8
Sept.	28·7	92·0	34·7	42·6	19	4	36·1	26	0	39·4	79	5·6
Oct.	25·9	92·0	55·9	36·7	31	3	21·9	35	0	32·8	76	2·8
Nov.	25·7	89·0	38 1	27·1	37	10	22·0	39	1	37·2	80	2·2
Dec.	25·0	87·0	17·3	21·1	45	28	17·7	67	10	38·3	88	1·1
Whole Year			225			114			89			57

The reflection of light from the underside of a leaf of *S. pilifera* or *S. lepidophylla*, as seen under the low power of the microscope, is confined to the ventral leaves. Chlorophyll and living protoplasm are absent, the cells are colorless, with the exception of those cell-groups exposed to the extreme action of the sun, which have their walls impregnated with a red-brown pigment. Only small sections which are covered by a part of the succeeding leaf remain green and are alive. In their natural environment the ventral leaves become mainly agents of reflecting light, instead of producing organic compounds under influence of the light. This production is taken over by the entirely green dorsal leaves, which explains their being in comparison to the ventral leaves much larger than those of the hygrophytic species. Fig. IX, 1, 2 shows a

part of the underside of a ventral leaf; (a) being very much exposed to the sun's rays has a red-brown color; (b) which was less exposed is white and glossy, both (a) and (b) reflecting the light; (c) remains green having been deeply shaded by a part of the next leaf, and possesses living protoplasm. A cross section of the leaf shows that none of the tissues under (a) and (b) contain any chloroplasts, only some grayish bodies in the cells which may indicate their presence at an earlier stage of development; very young leaves which are developed during the rainy season are

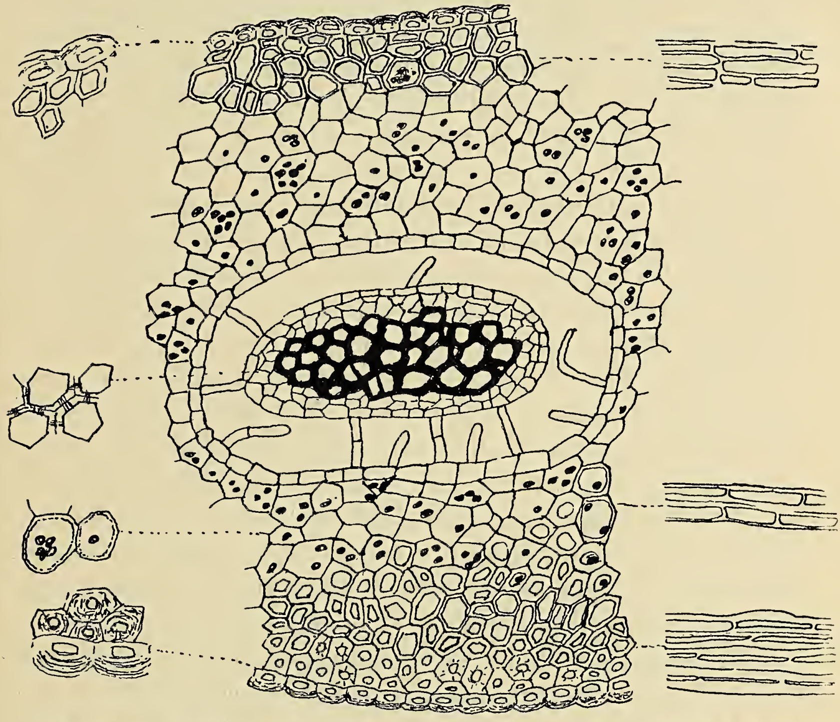


FIG. VII. Section of stem of *Selaginella pilifera* from moist and shady greenhouse. Note difference of cell walls of upper and lower surface.

entirely green. These chloroplasts must have been destroyed by the intense light; thus if parts of leaves which shade green portions of the succeeding leaf are removed, after a short time the exposed parts also become colorless and soon light reflecting.

Leaves of plants developed in a moist and shaded greenhouse are entirely green, with the exception of two rows of cells on the margin which are colorless.

Moreover the writer found on desert plants which are very much exposed that the underside is covered with a hard translucent

colloidal layer, which contributes very much towards its protection from extreme transpiration ; plants from more favourable situations do not possess such a layer. This can easily be detected with low powers of the microscope, and readily removed from the underside of the ventral leaves, clearly showing the imprints of the elongated cells of the epidermis. In contact with water the colloidal layer very quickly absorbs the liquid, losing the cell imprints, increasing five to six times in size, and slowly forms a structureless gelatinous substance. The colloid absorbs a weak solution of eosin, staining red in a short time, while the surrounding water remains pink. Water evaporates more slow from this gelatinous matter than pure water would do. This fact can be readily observed on the plant. There is no doubt that the colloidal layer has two functions to perform; in the first place it protects the plant against extreme heat, through minimizing transpiration by covering such parts of the plants by a hard substance; in the second place it absorbs the water after a shower or heavy dew and retains it longer than if the plant were without the gelatinous cover. The thickness of this colloidal layer, when dry, is sometimes thrice that of the leaf which it covers.

In *S. lepidophylla*, the chlorophyll-free margins of the dorsal leaves toward the apex are broad (Fig. X. 3) and reflect the light; the author observed that this is of much importance during the early development of the young dorsal leaves toward the growing point of the stem, since each half developed leaf is protected against the light by the broad margin of its neighbouring leaf. This feature is only of use when the branches are spreading in a horizontal direction, as they do when moistened.

The leaves of *S. Pringlei* have instead of a broad chlorophyll-free margin, a long awn at the apex (Fig. X, 1, 2); when the leaves are young, the awns of several leaves are situated close to each other toward the top of the shoot (Fig. I, 4), thus protecting the very young leaves. Also the growing point of the main stem, in the centre of the plant, is thus thoroughly protected by the awns. At a later stage the awns become valueless.

When it rains the cluster-balls soon unfold. This movement manifests itself in 1 to 2 hours, the whole plant becoming a flat rosette in 10 to 12 hours. The absorption of water by the tissues increases the weight of the plant by approximately 50 per cent, as is shown from the following table.

Increase in Weight due to absorption-water after moistening for two hours.

	Condition	Increase of weight		Condition	Increase of weight
S. lepidophylla	dead	48·6%	*S. convoluta*	dead	54·0%
S. lepidophylla	living	51·0%	*S. imbricata*	dead	52·5%
S. pilifera	dead	42·0%	*S. Pringlei*	dead	51·0%
S. pilifera	living	45·0%	*S. longispicata*	dead	47·2%
S. cuspidata	dead	43·4%	*S. longispicata*	dead old stem	40·0%
S. cuspidata	living	46·0%	*S. iuvolvens*	dead	47·2%

Shoot apices (including fully developed shoot) 15 mm. in length were used for these experiments. An old stem of *S. longispicata* of the same length showed a slightly smaller increase. It will be seen that living plants absorb slightly more water than dead plants.

The morphological and anatomical structure, especially of *S. lepidophylla* has been frequently discussed, *e.g.* by Hieronymus in Engler and Prantl "Die Natürliche Pflanzenfamilien" (7), Lotsy (15), Neger (18), and others. Original investigations were conducted by Leclerc du Sablon (14) and especially by Wojinorvić (29). I have carefully examined the work of the two last authors and compared their results with related species. Some of the results are correct, but other very important deductions have proved to be misconceptions.

Wojinorvić states that the main axis of *S. lepidophylla* has a spiral form, due to a different development of one of the two shoots. This interesting account, can only be expressed to the best advantage in his own words: "Die Entstehung dieser eigentümliche Form der Axe ist morphologisch so zu erklären, dass am Vegetations-punkte dichotomisch zwei Aeste angelegt werden, von denen der Rechte kräftiger wächst und strahlenförmig nach Aussen abliegend, als Seitenzweig auftritt, der Linke dagegen stellt die Verlängerung der Stammesspitze dar und wachst, nicht in derselbe Ebene bleibend, langsam nach oben, indem er sich dabei gleichzeitig spiralig nach innen dreht."

Through repetition of this kind of growth, as explained above, the peculiar spiral arrangement of twigs round the axis takes place. I clearly observed the same principle in other Selaginellas, e.g., *S. pilifera*, *S. Pringlei*, *S. involvens*, *S. cuspidata*, and *S. longispicata*, but was unable to find this development in *S. imbricata*. This characteristic seems peculiar to these species of Selaginella and has not been observed in other plants.

To explain the hygrochastic movement of the stem it is necessary to understand the anatomical structure. Leclerc du Sablon (14) states it is due to a difference in thickness in the cell walls on the two sides of the stem; the upper side, he says, is thick-walled, the lower thin-walled. Wojinorvić (29) is of the same opinion: "Die organisch Obere, bei der Zusammenrollung der Pflanze einwärts gekrümmte und daher concav werdende Seite wird aus Zellen mit stärken verdickten Wänden gebildet als die organisch Untere, bei der Zusammenrollung äussere, also convex werdende

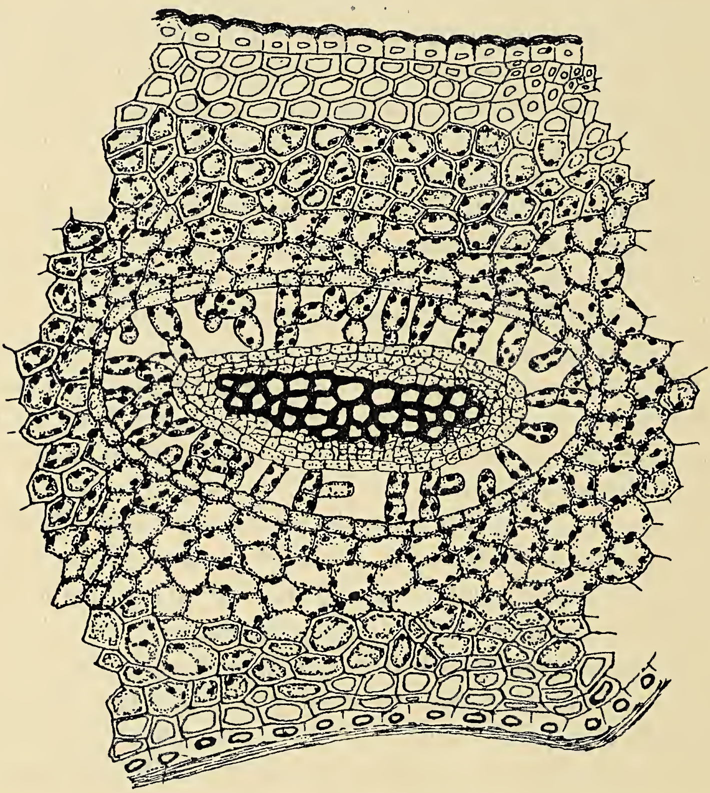


FIG. VIII. Section of stem of *Selaginella pilifera* from moist and shady greenhouse. Note similarity of cell walls of upper and lower surface.

Seite." He states further that the thick-walled cells absorb more water than the thin-walled ones and the former lose more water during drought than the latter, causing the plant to curl up and to have the appearance of a cluster-ball.

I found after careful examination that the tissues are neither thicker-walled on the upper nor thinner-walled on the lower side of the stem, but precisely the reverse and also that the thin-walled

tissue absorbs more water than the thick-walled. A close observation of transverse and longitudinal sections of the stem of *S. cuspidata*, *S. pilifera* (Fig. VII), *S. lepidophylla*, *S. Pringlei*, and *S. longispicata* from extremely exposed situations shows that on one side of the stem the cell walls are deep red brown and on the other side of the stem the cell walls are colorless; the ventral leaves are also partly brown or red brown, while the dorsal leaves are green. On longitudinal sections the red brown cells of one half of the stem are easily seen to be on the same side as the red brown celled leaves; on the other hand the colorless part of the stem carries the green leaves. On cross section it is at once evident that the colorless part is thin-walled and the red brown part of the stem is thick-walled. Consequently the former belongs to the uppermost part of the stem, the latter forming the lower surface of the stem.

The thick-walled cells are to be found in the epidermis, hypodermis and the outer cortex; the room in the cells is very much reduced; the walls clearly show secondary layers; the inner cortex is thinner-walled. When the stem becomes older, the whole of the inner cortex also becomes very thickwalled, with the exception of about two rows of cells toward the bundle. The epidermis of the upper side is almost as thick as that of the lower surface, but the cell walls of the hypodermis and cortex are considerably thinner. Moreover the thick-walled cells are much more suberized than the thin-walled ones. It follows that the thin-walled upper surface loses more water during drought, and absorbs more when moistened than the thick-walled tissues of the lower surface, and that this causes a corresponding curling up and spreading out of the shoot.

When a longitudinal section of a stem is observed in water, the thick-walled and thin-walled tissues appear to be of the same length; when dry the thick-walled side is longer than the thin-walled one; a difference which is considerably more pronounced on gently heating on a glass plate above a flame. When water is added to the dry slide, it is at once noticeable under the microscope that the thin-walled tissues absorb much water and increase appreciably in length; the thick-walled tissues, on the other hand, which during drought were curved toward the thin-walled, absorb very little and are straightened out again by the increase in length of the thin-walled tissue. The length of the tissues when dry and when moistened are summarized in the following table:

Length in mm. of longitudinal sections of full-grown stems of xerophytic Selaginellas.

Name	Condition	Wet	Dry	
		Equal length of both tissues	Length of thick-walled tissues	Length of thin-walled tissues
S. pilifera	dead, from Mexico	·900	·885	·835
S. pilifera ...	living, from greenhouse	1·200	1·190	·1140
S. lepidophylla	dead, from Mexico	1·000	·985	·935
S. lepidophylla	living, from desert region	·900	·880	·820
S. cuspidata	dead, from Mexico	·900	·880	·825
S. cuspidata	living, from greenhouse	1·000	·975	·950
S. longispicata	dead, from Mexico	1·000	·975	·930
S. Pringlei	dead, from Mexico	·900	·885	·840

The movements of the tissues are entirely mechanical, as their cells when old do not contain living protoplasm even in living plants: moreover similar results are obtained in dead plants as is shown in the table. They depend upon the hygroscopic capacities of the tissues, being entirely physical instead of biophysical. After drying above a flame, the tissue soon absorbs moisture from the surrounding atmosphere in a damp climate.

In *S. pilifera* there is a well developed lacuna with well formed one or two-celled trabeculæ round the bundle; the trabeculæ are thinner in individuals grown in a moist and shady environment. The proto- and metaxylem is well developed, although in proportion to the water supply of the stem.

Plants which were grown in a Wardian case in a moist and shaded greenhouse at Kew show different structural characters. The leaves are further apart and do not lie so flat against the stem (Fig. I, 1, 2). The cell walls of the epidermis, hypodermis and cortex are considerably thinner; the cuticle however is only slightly thinner. There is not much difference in thickness of the walls between the tissues of the uppermost part and the lower surface; consequently the stems do not fold up so much when dry. The tissues of the lower part of the stem are not impregnated with red brown pigment. Moreover the presence of suberin is less pronounced than in plants grown in a semi-arid environment. The intercellular spaces are larger and persist longer in plants grown in the greenhouse; also protoplasm remains longer in the cells of

the hypodermis and cortex (Fig. VIII). The xylem is of the same width but its elements are more numerous.

A section of the desert-grown ventral leaf shows a considerable thickness in both cuticles, especially the parts directly exposed to the sun's rays; the epidermis is thick-walled. The same tissue of the plant from the greenhouse is thinner and contains less suberin; the mesophyll of the former is composed of oval cells with small intercellular spaces; tha mesophyll of the latter has larger air-spaces (Fig. IX, 2, 3). The stomata appear toward the middle of the

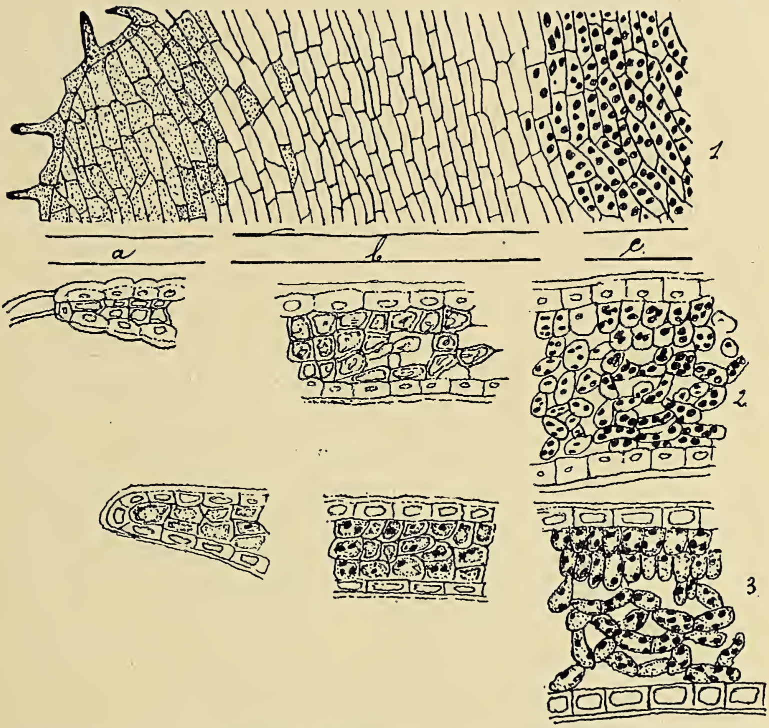


FIG. IX. Leaf of *Selaginella pilifera* 1, longitudinal view; 2, cross section; *a* and *b* exposed to intense sun's rays of which *a* has brown cell walls, only *c* has chloroplasts; 3, cross section of leaf developed in shade, all cells of mesophyll possess chloroplasts.

aligular side, being more numerous on a plant developed in the moisture. A very few stomata appear on the ligular surface of both kinds of leaves, although their influence upon transpiration and movement of gases can be but small. The cells toward the wings or margins of the leaf contain only one or two big chloroplasts, sometimes none, instead of 8 to 12 as in the other cells of the mesophyll. The dorsal leaves of both plants from the desert and from the greenhouse have a more pronounced spongy

parenchyma, which is thicker and here and there contains large air spaces. Although the anatomical construction of the stem of *S. pilifera* and *S. lepidophylla* differ but slightly, the leaves of the latter possess more elongated cells in the mesophyll. In *S. Pringlei*, the cells of the hypodermis and cortex also are similar (Fig. XI, 1) to those of *S. pilifera*, but there are 5 to 7 rows of cells in *S. pilifera* and *S. lepidophylla* from 7 to 9. Other species, e.g., *S. involvens*, *S. longispicata*, and *S. convoluta* possess the same characteristics as *S. pilifera*. There is, however, one striking difference in *S. imbricata*; specimens of which from Arabia, Zambesia and Abyssinia were examined. Individuals do not form flat, dense rosettes, like the other species of this group; the stems are more or less erect; the lower part is not branched but only covered with a few scale-like leaves (Fig. XI, 5). The upper half of the stem is branched as in other species. The various tissues are here similar to *S. pilifera*. The almost leafless and thick stem, is very hard and the cells are extremely thick-walled; the cells of the epidermis are smaller than those of the hypodermis. There is no difference in size between the cells of the hypodermis and most cell layers of the outer cortex; toward the centre the inner cortex becomes thin-walled (Fig. XI, 4). All the cells contain a large amount of oil; especially those of the thin-walled cortex. The cell walls of both sides of the lower stem are of the same thickness (Fig. XI, 2, 3) in all tissues. In the upper half of the stem, which is much branched and covered with both kinds of leaves, there is a marked difference in thickness in cell walls (fig. XI, 6, 7) between the upper and lower surfaces of each branch, as has been described in *S. pilifera* and *S. lepidophylla*.

Comparing the xerophytic Selaginellas of Group II and III with the hygrophytic species, it is apparent that the same tissues are present in all plants, although in modified form, corresponding with their particular environments. Xerophytic species adapt themselves easily to very moist and shaded environment; on the other hand, hygrophytic species are unable to grow in semi-arid situations.

A striking difference between plants of two different environments is that all the elements of xylem are much wider in hygrophytic than in xerophytic plants, and this feature stands in close relation to the water supply of the plants; moreover xerophytic species which have grown in a moist atmosphere have a more pronounced proto- and metaxylem. The cells of the cortex

are all large and thin-walled in the hygrophytic forms, and thick-walled and small in the xerophytic ones, as can be seen in comparing *S. pilifera* (Fig. VII) and *S. Galeottei*, a hygrophyte (Fig. XII). The hypodermal cells of the latter are, however, thicker walled, than the cortex, but do not contain any suberin or only to a slight extent. The cuticle contains suberin. The difference in width of the xylem vessels and cortex cells is given below.

Width in μ of vessels of xylem and of cortical cells in Selaginellas.

Name	Environment	Width of vessels of xylem	Width of largest cortex cells
HYGROPHYTIC PLANTS.			
S. Galeottei	moist greenhouse	40–70	80
XEROPHYTIC PLANTS.			
S. pilifera	from desert	10–20	50
S. pilifera	from moist green-house	20–30	62
S. lepidophylla	from desert	10–20	52
S. cuspidata	from desert	10–20	50
S. Pringlei	from desert	15–30	55
S. sanguinolenta	from exposed rocks	8–10	30
S. rupestris	from exposed rocks	20–35	40
S. rnpestris	from greenhouse	25–42	45
S. arenicola	from sand barrens	20–30	40
S. densa	from exposed rocks	18-30	35
S. rupincola	from exposed rocks	20-30	40

The occurrence and number of stomata, which regulate to a considerable extent the transpiration of plants and the movement of water, are worth consideration. These stomata are all protected by a thick cuticle, which in species of Group I has a special air chamber, followed by a narrow passage through which the entrance between the two guard cells is reached. The situation of the stomata on the leaves is peculiar to each of the three groups. The most occur as a rule toward the midrib of the aligular surface of the dorsal and ventral leaves, since most air-spaces of the spongy mesophyll are to be found in this neighbourhood. The few stomata which occur on the ligular surface of both leaves have an unimportant rôle. The author in the following table summarises the presence of stomata in the plants with which he worked.

The principal question which arises after having studied xerophytic Selaginellas is the problem of the immediate protection and behaviour of the protoplasm of plants in desert and other semi-arid situations during extreme drought. Examining cells of above plants one notices a considerable number of large oval and round drops which ooze out of the open cells, when sections are

Occurence of Stomata on Leaves of xerophytic Selaginellas.

Name	Ventral Leaf			Dorsal Leaf			Environment and Locality
	Ligular Surface	Aligular Surface	Margin	Ligular Surface	Aligular Surface	Margin	
GROUP I.							
S. rupestris	none	pres.	none	none	pres.	none	Exposed granite rocks, Georgia, U.S.A.
S. rupestris	,,	,,	,,	,,	,,	,,	Shady moist greenhouse, Kew Gardens
S. rupincola	,,	,,	,,	,,	,,	,,	Exposed rocky place, desert, Tucson, Arizona, U.S.A.
S. arenicola	,,	,,	,,	,,	,,	,,	Dry pine wood, Florida, U.S.A.
S. densa	,,	,,	,,	,,	,,	,,	Exposed rocky place, Montana, U.S.A.
S. capensis	,,	,,	,,	,,	,,	,,	Exposed place, Orange River Colony, S. Afr.
S. Mildei	,,	,,	,,	,,	,,	,,	On rocks, San Luis, Brazil.
GROUP II.							
S. borealis	few	pres.	none	few	pres.	none	Exposed rocks, Kamschatka.
S. saccharata	,,	,,	,,	,,	,,	,,	On bluffs, Guadalajara, Mex.
S. mongolica	,,	,,	,,	,,	,,	,,	On rocks, Hsai-Watai, China.
S. sanguinolenta	,,	,,	,,	,,	,,	,,	On rocks, Karrum Valley, Afghanistan.
S. Douglasii	,,	,,	,,	,,	,,	,,	On trees in forest, Oregon, U.S.A.
GROUP III.							
S. lepidophylla	few	pres.	none	few	pres.	none	Exposed rocks, Guadalajara, Mex.
S. pilifera	,,	,,	,,	,,	,,	,,	Exposed rocks, Sonora, Mex.
S. pilifera	,,	,,	,,	,,	,,	,,	Greenhouse, Kew Gardens.
S. convoluta	,,	,,	,,	,,	,,	,,	Rocky exposed place, Uraguay.
S. cuspidata	,,	,,	,,	,,	,,	,,	Lava fields, Tlalpan, Mex.
S. cuspidata	,,	,,	,,	,,	,,	,,	Greenhouse, Kew Gardens.
S. imbricata	,,	,,	,,	,,	,,	,,	Rocks, Mount Dijot, Arabia.
S. Pringlei	,,	,,	,,	,,	,,	,,	Exposed place, Santa Eulalia Mts., Mex.
S. involvens	,,	,,	,,	none	,,	,,	Exposed place, Amurland, Siberia.
S. longispicata	,,	,,	,,	few	,,	,,	Rocky place, Porfiric Valley, Mex.

cut for microscopic examination. Alcanna readily stains these drops red, which is evidence of the presence of oil. This oil is to be found in very small drops in the protoplasm when examined in water; when the cell loses water or, during plasmolysis, the protoplasm shrinks, these drops get larger through union of several small ones. In what form oil is present when the cell has lost all its available water could not be observed, but the writer suggests that a film of oil forms around the entire protoplast or at least its vital parts, which is then able to enter the dormant state during drought; this condition is very likely the same as that of matured seeds, and especially those of Cruciferous plants. Neither

hygrophytic species nor xerophytic plants grown in a moist environment produce oil; the main product of C,H, and O is starch which is, however, less present in xerophytic plants grown in exposed places. This suggests that oil is a protection as well as a reserve food. Dead cells, like those of certain parts of the thick-walled cortex and especially of the hypodermis possess very large drops of oil, which frequently occupy the entire width of the cell.

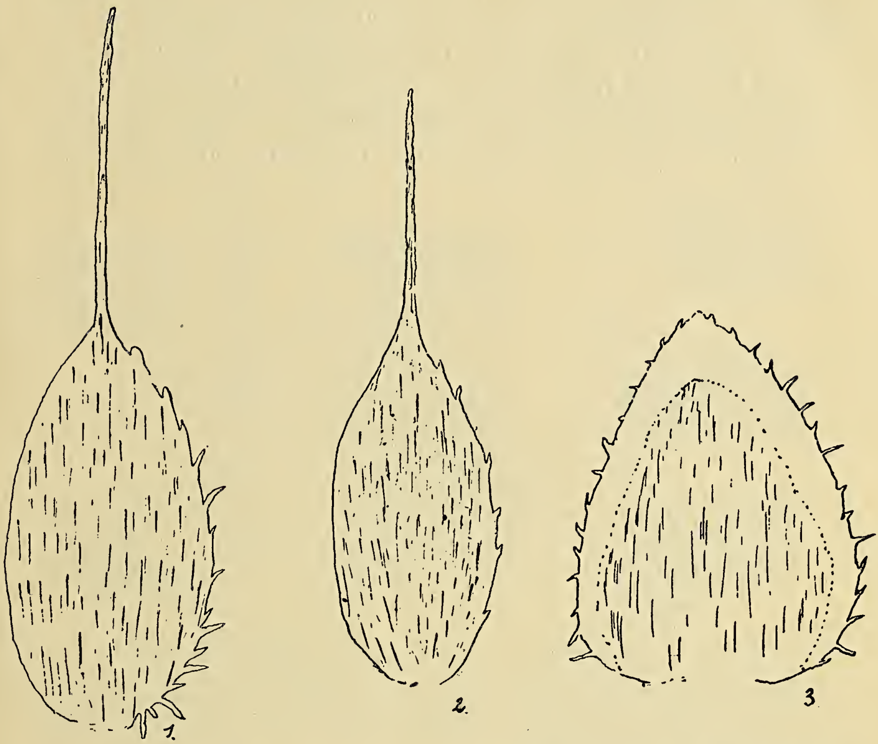


FIG. X. *Selaginella Pringlei*, 1, ventral leaf; 2, dorsal leaf. *Selaginella lepidophylla*, 3, ventral leaf.

The writer's study of the behaviour of xerophytic Selaginellas leaves many questions unanswered, among which the structure and action of the roots and rhizophores is of first importance, as is also a comparative study of osmotic pressure in cells of plants grown in the desert and in a moist atmosphere; further the development of the gametophyte and a closer study of photosynthesis have to be considered. Satisfactory results can only be obtained when plants are studied in their natural environment.

SUMMARY.

About six per cent of the known species of *Selaginella* are xerophytic. Their geographical distribution is closely associated with that of xerophytic ferns.

Comparing various species of xerophytic and hygrophytic Selaginellas one notices the very close proximity of the dorsal and ventral leaves in the former and the great distance between the succeeding leaves in most species of the latter. There is a striking similarity in the size of the leaves of all xerophytic species, while in all hygrophytic Selaginellas there is a great difference in the size of dorsal and ventral leaves. This similarity in size of leaves of xerophytic forms is of much importance from the photosynthetic standpoint; the ventral leaves produced under the influence of this

FIG. XI. *Selaginella Pringlei*, 1, epidermis and hypodermis. *S. imbricata*, 2 and 3, opposite sides of lower part of the stem, showing epidermis and hypodermis, both have cells with thin walls; 4, section of middle portion of stem; 5, part of lower half of the stem; 6 uppermost, and 7, lower surface of the stem above the middle. Note difference in thickness of cell walls of the uppermost part and lower part of the stem.

extreme environment contain but few chloroplasts, and most of the production of organic matter has to take place in the comparatively large dorsal leaves.

There are three groups of xerophytic Selaginellas. (1) Plants with vertical leaves, of the same shape and size. The apex of each leaf ends in a long awn containing no chloroplasts. The anatomical construction is sclerotic. (2) Plants having slender, wiry trailing stems, spreading over the ground or hanging from rocks and sometimes trees. (3) Plants having a spreading habit, stems often forming a flat, dense and close rosette, rolling into a cluster-ball during drought.

In the first group, the leaves, which stand in a vertical direction and are parallel with the stem, form a protection against the intense sun's rays. The growing points of the stems receive the rays directly, but the bundle of awns situated on the apex of the

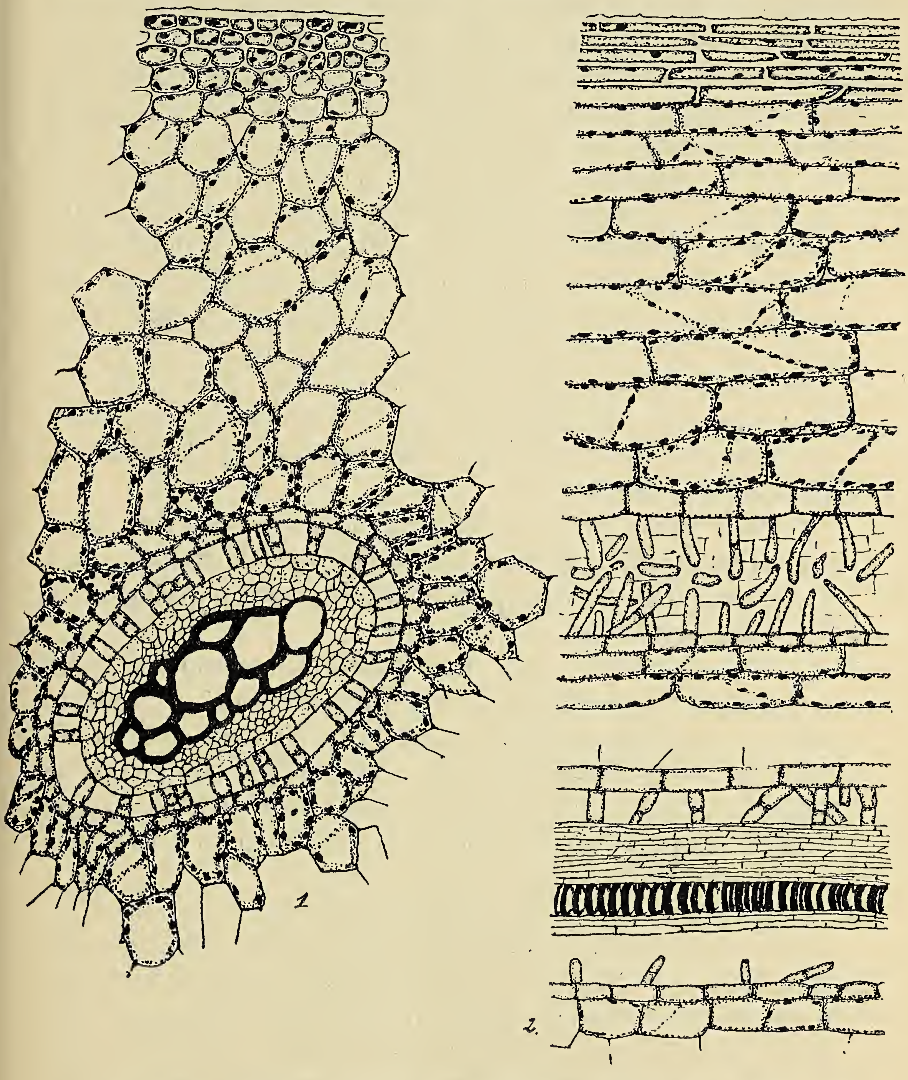


FIG. XII. *Selaginella galeottei*, a hygrophytic species from shady and moist greenhouse. Note large and thin-walled cells of hypodermis and cortex, and well developed xylem in comparison with *S. pilifera*, 1, cross section ; 2, longitudinal section.

leaves reflect the light entirely. All plants have a thick-walled epidermis, hypodermis and outer cortex, which are heavily impregnated with suberin. The leaves are all surrounded by

a thick-walled epidermis; the wings contain a well developed sclerotic tissue, all heavily suberized. The elements of the proto- and metaxylem are considerably narrower than those of hygrophytic species. Plants which were grown in a moist shady greenhouse develop horizontal leaves; the various tissues are neither as thick-walled nor as heavily suberized; the xylem has wider vessels. Some species are petrophilous, other are decidedly psammophilous.

The second group is composed of plants with a spreading habit; some show affinities with the last group, since they are able to roll up during drought. The anatomical construction is not as sclerotic as in the previous group, although the walls of the epidermis, hypodermis and outer cortex are very thick-walled. Some species produce a red pigment which is deposited in the cell walls of very exposed stems. In some forms the vessels of the xylem are very narrow, which is correlated with the low water supply and the very small leaves of the plant. The cuticle and other walls of the epidermis of the leaves are extremely thick. The mesophyll is well developed and possesses large air-spaces in the spongy parenchyma.

Plants of the last group are exceedingly well fitted for a semi-arid environment. The stems are densely tufted and curl up into a more or less close cluster; the leaves are placed horizontally on both sides of the stem.

During intense heat the exposed parts of the stem and leaves reflect the light considerably; these parts are white or brown to red-brown, according to their exposure to the heat. The brown color is always in the cell walls. On very exposed places the underside of some species is protected by a colloidal layer against extreme transpiration, and this retains the water for a long time when moistened.

The anatomical construction of all species shows a rather thin-walled hypodermis and cortex on the upper (inner) surface of the stem, and a thick-walled hypodermis and cortex on the lower (outer) surface. During drought the thin-walled tissue loses more water than the thick-walled tissue, which causes the plant to curl up; it absorbs more water when moistened which causes the plant to spread out. The statements of Leclerc du Sablon and Wojinorvić are misconceptions. These investigators state that the thick-walled tissues are on the upper side of the stem and absorb more water than the thin-walled tissues when moistened, and lose more water when drying. The hygrochastic movements are mechanical and can be also observed on dead plants. The plants increase in

weight after complete absorption of water from 42 to 54 per cent.

Xerophytic Selaginellas contain in their cells a considerable amount of oil; it is to be found in small drops in the protoplasm; when the cell loses water and the protoplasm shrinks, the drops unite and become larger, which suggests that a film of oil forms around the entire protoplast during drought, when it is able to enter its dormant state. Hygrophytic species do not produce oil, but starch, and this suggests that oil is also a reserve food for the xerophytic species, which produce less starch.

LITERATURE.

1. Baker, J. G. Handbook of Fern Allies, London, 1887.
2. Campbell, D. H. Structure and development of mosses and ferns, New York, 1905.
3. Christ, H. Die Geographie der Farne, Jena, 1910.
4. Cornaille, F. Note sur la structure de la fronde dans le genre de Selaginella, Bull. Soc. Roy. de Bot. de Belgique XXXVI: 100, 1897.
5. Coulter, John M. Botany of Western Texas, Contr. Nat. Herb. Washington, 1892.
6. De Bary. Vergleichende Anatomie der Gefässpflanzen, Leipzig, 1879.
7. Engler and Prantl. Die Natürlichen Pflanzenfamilien, I, 4 : 6 21, 1900.
8. Eseltine, G. P. van. The Allies of Selaginella rupestris in South Eastern United States, Contrib. Nat. Herb., Washington, 1918.
9. Gibson, R. J. H. Contributions toward a knowledge of the anatomy of the genus Selaginella. Ann. of Bot. VIII: 131, 1894; X: 77, 1896; XI: 123, 1897.
10. Gibson, R. J. H. On the silicious deposits in the cortex of certain species of Selaginella. Ann. of Bot. VII; 355, 1893.
11. Haberlandt, G. Physiological Plant Anatomy, London, 1914.
12. Haberlandt, G. Die Chlorophyllkörper der Selaginellen. Flora LXXI; 291, 1888.
13. Kamerling, Z. Zur Biologie und Physiologie der Zellmembran. Bot. Centralbl. LXXII; 53, 1897.
14. Leclerc du Sablon. Revivescence du Selaginella lepidophylla, Bull. Soc. Bot. de France, XXXV; 109, 1889.
15. Lotsy, J. P. Vorträge über Botanische Stammesgeschichte, Jena 1909.
16. McDougal, D. T. Botanical Features of North American Deserts, Washington, 1908.
17. Mitchell, G. Contributions toward a knowledge of the anatomy of Selaginella, Ann. of Bot. XXIV; 19, 1910.
18. Neger, F. W. Biologie der Pflanzen, Stuttgart, 1913.
19. Schaede, R. Zur Biologie einiger xerophile Farne, Cohn. Beitr. Biol. d. Pfl. XI; 107, 1912.
20. Schimper, A. F. W. Pflanzengeographie auf physiol. Grundl. Jena, 1908.
21. Seyd, W. Zur Biologie von Selaginella, Jena, 1910.
22. Spalding, V. M. Distribution and movements of desert plants, Washington, 1909.
23. Steinbrinck, C. and H. Schinz. Ueber die anatomische Ursache der hygrochastische Bewegungen der sogen, Jerichorosen. Flora XCIII; 471, 1908.
24. Treub, M. Recherches sur les organes de la végétation du Selaginella Martensi, Musée Bot. de Leide, 1877.
25. Underwood, L. M. Selaginella rupestris and its allies. Torr. Bot. Club XXV; 125, 1898.
26. Uphof, J. C. Th. Die Pflanzengattungen, Leipzig, 1910.
27. Volkens, G. Flora der ägyptisch-arabishe Wüste, Berlin, 1887.
28. Warming, E. Ecology of Plants, Oxford, 1909.
29. Wojinorvić, W. P. Beiträge zur Morphologie, Anatomie und Biologie von Selaginella lepidophylla, Breslau, 1890.
30. Wooton and Stanley. Flora of New Mexico, Washington, 1915.

MUTATIONS AND EVOLUTION.

BY R. RUGGLES GATES.

CHAPTER IV.

NON-DISJUNCTION IN DROSOPHILA.

ANALOGOUS to the irregular distribution of meiotic chromosomes, which gives rise to such mutants as *Œnothera lata* and *Œ. scintillans*, is the phenomenon in *Drosophila* which Bridges (1916) has called non-disjunction. To make this matter clear it must be remembered that *Drosophila melanogaster* has four pairs of chromosomes of different sizes, including a pair of sex chromosomes XX in the female and an unequal pair XY in the male. These pairs separate like the others in meiosis, so that half the sperms have an X chromosome and half a Y, while all the eggs after maturation have an X. Furthermore, we need to know that the Y chromosome, as in other insects, is inactive, carrying no known factors and taking no active part in sex-determination. A large number of sex-linked characters are now known, including many eye colours, and as these characters are distributed in crosses exactly as the X chromosomes are distributed—each daughter receiving one X from her father and one from her mother while each son receives his single X from his mother—we must suppose that sex-linked characters are determined by the presence of the X chromosome and that, in short, the determiners for such character-differences are borne by the X chromosomes. Moreover, the phenomena of "crossing over" or separation of two sex-linked characters which went into the cross from the same parent, *i.e.*, carried by the same X chromosome, determine the relative position of such determiners in the chromosome, on the assumption that the farther apart they are along its length the more frequently crossing over (from the wrapping of the chromosomes around each other and subsequently breaking apart in new positions) will take place. On the basis of the percentages of crossing over, chromosome maps have been constructed for all four chromosomes, in which are indicated the relative positions of the various genes or determiners along their length. It will be understood that crossing over occurs between the members of a pair of chromosomes, but not between one pair and another. The amount of breeding work involved in thus determining that all the mutations fall into four linkage groups and the relative positions of the members of each group with reference

to each other, has been prodigious and is an achievement in itself. The data for sex-linked characters alone involved the breeding of over half a million flies.

Chromosome No. 1, the X, (see Morgan *et al.* 1915), contains all sex-linked mutations, since this is the sex chromosome. Such factors already number over 50, including a series of eye colours, bar eye with a reduction in the number of facets, yellow and sable body colours, forked bristles, club, miniature and rudimentary wings, and several lethal factors which prevent development when present in the homozygous condition. Chromosome No. 2 is the longest pair and contains such mutation factors as purple eye, curved and vestigial wings, and black body. No. 3, the next longest, as shown by linkage percentages, contains such eye colours as pink and peach, rough eye due to a peculiarity of the facets, ebony, sooty and sepia body colours, and beaded wings. The fourth group of factors, more recently discovered, and transmitted independently of the others in the Mendelian sense, contains only two known factors, bent wings and the eyeless condition. It evidently corresponds with the fourth, very small, pair of chromosomes.

It has long been known that crossing over, which may occur between the various members of each group, is confined to the female. The amount of crossing over is also independent of the way in which the factors enter an individual in a cross. Thus if they enter from the same parent (*i.e.*, in the same chromosome) any two factors tend to cross over with a certain frequency, while if they enter from different parents they tend with equal frequency to cross over so that both will be in the same chromosome in the offspring. In the male of *Drosophila* there is no crossing over between the X and Y or between any other pairs of chromosomes.

The probable reason for this has only recently been discovered (see Doncaster 1920, p. 235) by Metz. It apparently depends upon the fact that while in the egg there is a stage during maturation when the long, thin chromosomes are twisted round each other, there is no such stage in the male during the period preceding the separation of the chromosome pairs, the chromosomes remaining in a fairly condensed state during the whole growth period of these nuclei. Once again cytology furnishes the basis for the peculiarities in the phenomena of inheritance observed. In some other organisms (moths and fowls) crossing over takes place only in the male and not in the female, while in *Primula*, grasshoppers and rats it takes place in both sexes. That crossing over involves a break n the chromosome at a definite point, and not an indiscriminate

exchange of genes between a pair of chromosomes, is shown by the fact that when a number of factors are involved whose position at intervals along the chromosome is known from the crossing over percentages, a group of them go over *en bloc* and the rest remain in the chromosome (*i.e.*, group) where they were before. Thus (Morgan *et al.* 1915, p. 66) if a hybrid female is made up, having received from her mother the mutant factors yellow, white, abnormal, bifid, vermilion, miniature, sable, rudimentary, and forked, and from her father the normal allelomorphs of these together with the dominant mutant factor for bar eye, her formula may be written as follows: $\frac{\text{y w a b}_i \quad \text{v m s} \quad \text{r f b}'}{\text{YWAB}_i \quad \text{VMS} \quad \text{RFB}'}$ these factors all being present in the two X chromosomes. When such females were bred, they were found to produce the following kinds of eggs, with the frequency indicated:

Non-crossover eggs.

y w a b_i	v m s	r f b′	— 6
$YWAB_i$	VMS	RFB′	— 8

Single-crossover eggs.

YWa b_i	v m s	r f b′	— 2
$YWAB_i$	v m s	r f b′	— 2
y w a b_i	VMS	RFB′	— 2
$YWAB_i$	V m s	r f b′	— 1
$YWAB^i$	VMS	r f b′	— 1
y w a b_i	v m s	RFB′	— 1

Double-crossover eggs.

y w a b_i	VMS	RFb′	— 1

But such types as $yWaB_i$ VmS rfB′ were not found, showing that indiscriminate reassortment of the factors between a pair of chromosomes does not occur.

Double crossing over, in which the ends of a pair of chromosomes exchange while the central portion remains as before, lessens the effect of single crossovers and so is called interference. The result is as though the percentage of crossing over between certain points was reduced.

Now if a female with vermilion eyes is crossed with a wild red-eyed male, the vermilion being recessive the daughters will have red eyes like their father because they received his X chromosome with the red factor which is dominant to vermilion. But the sons will have vermilion eyes like their mother, since they received her X chromosome and only the inactive Y from the father. This criss-cross inheritance will always happen when the

father bears a dominant sex-linked character. About 50 such sex-linked mutations are now known in *Drosophila.*

But occasional exceptions occur, in which a female produces a daughter like herself or a son like the father. These primary exceptions by an ordinary XX female were found to be the result of an egg in maturation either retaining both X chromosomes or allowing both to pass out into the polar body. Such an egg will be XX or zero as regards its sex chromosomes. If such eggs are fertilized by ordinary sperm from a red-eyed male, the result will be as

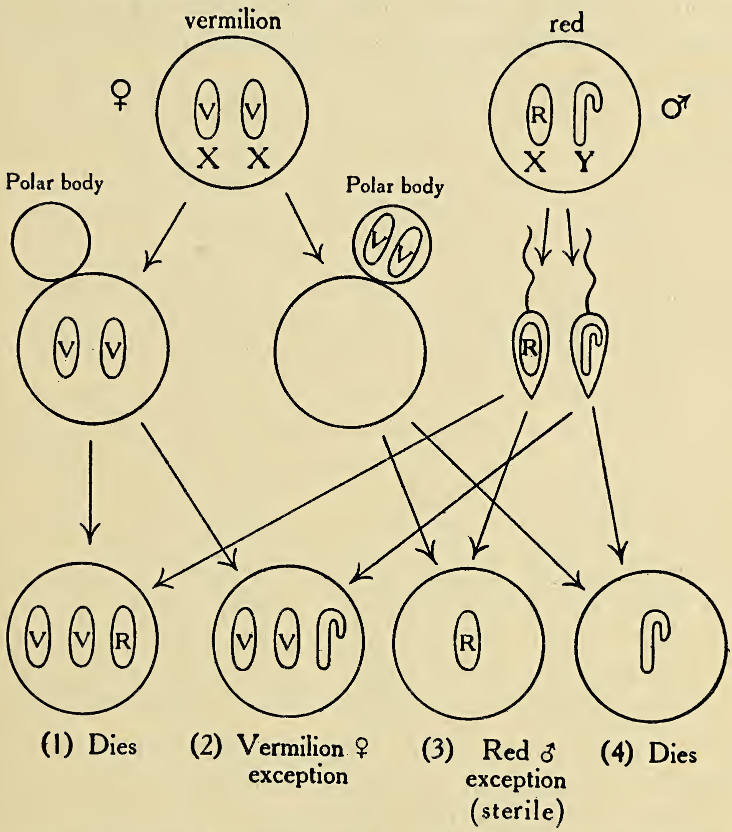


Fig. 1. Diagram of primary non-disjunction. Modified after Bridges.

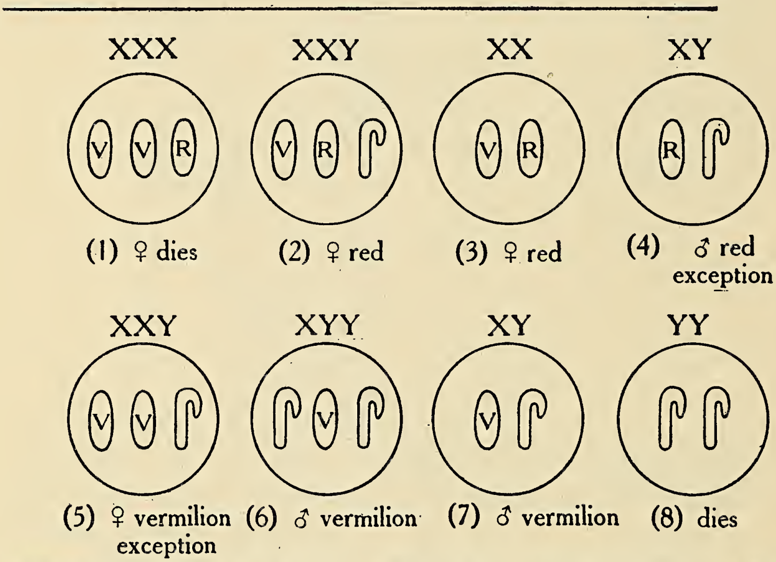
shown in the diagram (Fig. 1). Four new types will result: (1) The XX egg + X sperm = XXX females which die. (2) The XX egg + Y sperm = XXY female having vermilion eyes and hence an exception to the criss-cross rule. (3) The O egg + X sperm = XO male which is sterile. It has red-eyes and is a patroclinous exception to the criss-cross rule. (4) The O egg + Y sperm = OY zygote which is not viable. Hence only

half of the primary exceptions survive. The XXY females are fertile and can be used for further breeding.

Non-disjunction also occurs in the male, giving XY and O sperm. The XY sperm would produce XXY daughters, like the XXY females above but with red eyes. They are therefore not exceptions, but will give exceptions in their offspring. Wilson (1909) observed three spermatocytes of Metapodius, another insect, in which X and Y went to the same pole in the reduction division. The XXY females give about 4% of secondary exceptions (*i.e.*, 4% of daughters like the mother and 4% of sons like the father) when crossed with a male having other sex-linked characters. This was

Eggs XX XY X Y

Sperms X Y



at first supposed to be due to a *factor* for non-disjunction. The exceptions were afterwards found to be due to the presence of the Y. After further breeding experiments it was predicted that cytological examination of the daughters of an exceptional female would show the presence of an extra chromosome in half the daughters while the other half would be normal. This prediction was completely verified.

Let us consider now what will happen in XXY females. Synapsis may take place between the two X chromosomes, leaving the Y unmated (homosynapsis), or it may be of the XY type (heterosynapsis). About 84% of the cases were formed by breeding

to be homosynaptic. After heterosynapsis the reductions will be XX—Y or X—XY. From the former the eggs after maturation will be $\frac{1}{2}$XX and $\frac{1}{2}$Y; from the latter, $\frac{1}{2}$X and XY. Also from homosynapsis, the reductions will be X—XY or XY—X, since the unmated Y may remain in the egg or enter a polar body, and the eggs will therefore be $\frac{1}{2}$X and $\frac{1}{2}$XY. Hence 4 classes of eggs result: XX and Y 4% each, of single origin; X and XY 46% each, of composite origin. Therefore if such an XXY female having vermilion eyes is crossed by a wild male (red eyes), there will be 8 classes of zygotes, as shown in the diagram (Fig. 2).

Of these eight classes, (2) are not exceptions but would produce exceptions in the next generation, (4) are produced by the reverse of the ordinary method, *i.e.*, by the union of a Y egg and an X sperm. While themselves exceptions, they are ordinary males and can neither produce exceptions nor transmit the power of doing so, (6) are not exceptions, but some of their daughters will get the extra Y (from XY sperm + X egg) and so produce secondary exceptions. It was found that homosynapsis occurs much oftener than heterosynapsis, but otherwise the chromosome distribution is according to chance. That matroclinous exceptions had developed from fertilised eggs was shown by the presence of paternal characters derived from other chromosomes.

In XYY males, synapsis may be of the XY or YY types. If these are simply by chance there should obviously be twice as many XY as YY synapses. The synapsed chromosomes disjoin and the other one apparently goes equally to either pole. Hence in XYY males 4 classes of sperm will be produced, X and YY from heterosynapsis (small classes) and XY and Y from homosynapsis (twice as large and from two sources). These four classes of sperm fertilizing an ordinary female would give the following results:

Sperm	X	YY	XY	Y
Eggs	X			
	XX	XYY	XXY	XY
	♀	♂	♀	♂

Half the daughters will therefore be XX and half XXY, while half the sons will be XY and half XYY, again producing exceptions. Primary non-disjunction in the female, or failure of the sex chromosomes to separate in the egg, occurred 12 times in breeding experiments involving 20484 flies, or 1 in 1700. The fact that XO males are sterile shows that the Y chromosome has some function in spermatogenesis, if only to serve as a balance wheel.

In the cytological examination one female was found with 10 chromosomes, *i.e.*, XXYY. She was from a stock culture in which half the females should be XXY and about half the males XYY. Nearly half the eggs of such females are XY, and one-third of the sperm of an XYY male are XY. Hence XXYY females should frequently occur in this stock.

The relations of non-disjunction to crossing over are still more intricate and surprising in their results. In XXY females, in cases in which the synapsis was XY (heterosynapsis) since the X chromosome was in synapsis with Y, there could be no crossing over with X. The XX eggs should therefore always be non-crossovers, and this was shown to be true. Linkage experiments show that there is about 33% of crossing over between eosin and vermilion, *i.e.*, if they entered the cross in separate X chromosomes one-third of the eggs would carry neither factor or both in their single X. But when an XXY female carried eosin in one of her X chromosomes and vermilion in the other, the exceptional daughters were always like their mother in that they still carried eosin in one X and vermilion in the other. On the other hand, in the XY and X eggs from an XXY female, crossing over took place in the ordinary way.

Such XXY females have been obtained from three sources, (1) XX egg + Y sperm, (2) XY egg + X sperm, (3) X egg + XY sperm. In all cases the frequency of secondary exceptions is the same, which means that the method of synapsis is the same whether the two chromosomes came from the same or from different parents.

One must agree with Bridges that these results, which are only summarized here, furnish a definite proof of the chromosome theory of heredity. Exceptions which seemed at first to be unconformable to any possible chromosome theory of heredity have turned out to be a brilliant confirmation of the whole position. In no other case have breeding and cytological work been combined with more convincing results. The correctness of the point of view involved has been independently demonstrated, first by breeding experiments and then by cytological observation.

There are certain interesting and significant differences between the results of duplication of a chromosome in plants and animals. As we have seen, individuals containing an extra Y chromosome in the nuclei, or even an extra X as well (XXYY), show no external peculiarity and are only distinguishable by the

differences they show in hereditary behaviour owing to the different factors they carry, or by actually counting their chromosomes. The same is true of Metapodius (Wilson, 1909), in which some individuals were found having as many as six supernumerary chromosomes owing to irregular distributions of the Y chromosome in the reduction division, yet they were apparently indistinguishable from others with the normal equipment of chromosomes. This is in contrast to the conditions in plants, where, as shown in Chapter III, the extra chromosome is constantly associated with new external characters. Whether this is a general difference between plants and animals is unknown, but it may result from the fact that the cell unit in plants is a more rigid thing and less subject to regulation (in the physiological sense) from the structural point of view.

In *Drosophila* then, the detection of the presence of an extra chromosome is only by means of the factors transmitted, or by direct observation of the chromosomes. In *Œnothera* there is also a difference in the hereditary behaviour, nearly all the 15-chromosome forms splitting at least into the two parental types. But in addition the external characters are directly affected. Although the breeding results with plants are necessarily much slower, yet it is hoped that the nature of the chromosomal differences between the various 15-chromosome types will ultimately be determined.

It has been necessary to dwell upon these results in *Drosophila* at some length, for although an animal it is obvious that the results concerning linkage, crossing over, lethal factors and the conceptions of the linear arrangement of factors in the chromosomes will fundamentally affect our conceptions regarding the basis of heredity and the constitution of the germplasm in plants as well. Indeed, this has already been the case. Once it is generally recognized that in the morphology and constitution of the chromatin lies the chief basis for the inheritance of differences, then we shall be on safe ground for future experimental progress.

CHAPTER V.

Parallel Mutations.

For many years *Œ. lamarckiana* was the only Œnothera known to exhibit mutations. Then mutations were discovered in a race of *Œ. biennis*, one of which showed all the peculiarities of *lata*, but had the small flowers and other specific features of *biennis*. From this form the conception of parallel mutations and the recognition of their significance originated (see Gates, 1912a). Shortly afterwards Stomps (1912a) described independently the mutants *nanella* and *semigigas* from hybrids between *Œ. biennis* and *Œ. biennis leptomeres* Bartl. (=*Œ. biennis cruciata* de V.) but apparently without recognizing the significance of their parallelism to forms derived from *lamarckiana*. *Œ. biennis* mut. *lata* was later[1] described in detail and shown to have 15 chromosomes. It was clear that the same kind of germinal change was involved in both species. Two other probable mutations in *Œ. biennis*, one a red-nerved form parallel to *rubrinervis* Gates, the other resembling *lævifolia*, were also obtained. On these results the conception of parallel mutations was founded, and it has since been generally adopted by mutationists (see Stomps 1914, de Vries 1915b).

Equally striking mutations have now been obtained from several species of Œnothera, including such wild species as *Œ. grandiflora*, *Œ. stenomeres* and *Œ. pratincola*. In the last two species, some of the mutations are parallel to those described in *Œ. lamarckiana* or *Œ. biennis*, others are entirely dissimilar. A number of cases of clearly parallel mutations are put together in Table II, but a great many cannot readily be arranged in a table, and these will be discussed separately. From the table it will appear that three species have produced *lata* mutations (with 15 chromosomes), while five have produced mut. *gigas* (28 chromosomes) or mut. *semigigas* (21), and the same five species have given rise to dwarfs. These mutations have also occurred in various crosses. Virescence has also appeared independently in three species of Œnothera.

Let us now consider the history of some of these mutations, especially in *Œ. biennis* Linn., *Œ. stenomeres* Bartl. and *Œ. pratincola* Bartl., all of which have small flowers, are self-pollinated and rarely undergo natural crossing. The writer (1912, 1914)

[1] Gates & Thomas 1914.

obtained mut. *lata* from *Œ. biennis*, also a red-nerved (*rubrinervis*) type and a *lævifolia*. Stomps (1912a), in the cross *Œ. biennis* × *Œ. biennis leptomeres* Bartl. (*leptomeres*=*Œ. biennis cruciata* de Vries) observed one dwarf mutant (*biennis nanella*) and one *semigigas* (with 21 chromosomes). The *biennis* parent was descended from a rosette collected by Stomps on the sand dunes near Wykaan-Zee in 1905, which gave a uniform race. The *biennis leptomeres* was derived from a plant originally collected in 1900 by Ernst de Vries near Santpoort, Holland, and from which a constant strain was obtained. In 1903, one dwarf (*Œ. biennis leptomeres nanella*) arose in about 600 of the tall cruciate variety. The original *leptomeres* plant, when found in 1900, was surrounded by a number of normal *biennis*, and evidently had arisen as a mutation.

TABLE II.

PARALLEL MUTATIONS IN ŒNOTHERA.

Species	*lata*	*gigas*	*semigigas*	Dwarfs			*cruciata*	*elliptica*	*lævifolia*	Virescence
				nanella	*semialta*	*debilis*				
Œ. lamarckiana Ser.	X	X	X	X			(X)[1]	X	(X)[1]	X
Œ. biennis Linn.	X		X	X			X		(X)[1]	X
Œ. grandiflora Sol.		X	X	X						
Œ. stenomeres Bartl.		X		X						
Œ. pratincola Bartl.		X								
Œ. Reynoldsii Bartl.		X?			X	X				
Œ. suaveolens Desf.	X									
Œ. multiflora Gates[2]										X
Œ. grandiflora × *biennis*[3] F$_2$ and F$_3$	X		X?	X				X?		

The significance of the various species and varieties with cruciate flowers will be considered later. The first experiments with pure *Œ. biennis* were undertaken by Stomps (1914). He collected a rosette of this species at Beverwyk, Holland, in 1905, from which he obtained a pure line. Among over 900 plants belonging to the third and fourth generations, Stomps found 6 mutants, 1 *nanella*, 1 *semigigas* and 4 *sulfurea*. The last differs from

[1] When enclosed in parentheses, the form is a presumptive mutation, but has not actually been obtained in a pedigree culture.

[2] For a description of this "species," probably of hybrid origin, see Gates, 1914b.

[3] Davis, 1913.

the type of *biennis* only in having pale yellow petals. It is found occasionally on the sand dunes and must have originated as a mutation.

The well-known uniformity and constancy of *Œ. biennis*, together with the apparent impossibility of crossing in the regions from which these plants were derived, greatly enhances the importance of the mutations obtained from them. This species, the only one with which Linnæus was at first acquainted, was originally brought from North America in 1614—the first evening primrose to be brought to Europe.[1] It was soon naturalized on the Dutch sand dunes, where it has retained its characters with remarkable uniformity for three centuries until the present time. Davis (1914) admits that no species in cultivation has greater claims to be regarded as a pure species, and at one time was willing to admit that if mutations were produced by it they would go far to prove the correctness of the mutation hypothesis that the production of new forms is not merely a phenomenon of hybridity. Indeed it would be difficult to find any species whose claims to "purity" or freedom from crossing are better authenticated. Not only is it self-pollinated, so that crossing would be a rare event at best, but for three centuries in these Dutch localities it has been more or less completely isolated from its American relatives. Even if its ancestors were crossed before they left America, 300 generations of self-fertilization would be more than ample to reduce it to a homozygous condition again,[2] unless a condition of balanced lethal factors maintained it in a heterozygous state.

But the Drosophila work shows (Muller, 1918)) that such a condition of balanced lethals is not the result of crossing, but of alterations which arise in the germ-plasm. Another fact against the hybridity theory is this. The mutant *sulfurea*, which has been shown to arise occasionally in cultures, is also "far from rare" on the Dutch dunes (de Vries, 1915b). Apparently it was first mentioned in 1687 by Hermannus in *Hort. Acad. Lugduno-Batavi*

[1] For the early history of some of these forms see *Mut. Factor*, p. 47.

[2] Without dealing with the mathematical formulæ for inbreeding involved (see East and Jones, 1919, p. 91), it may be pointed out that even if a large number of independent differences were involved in an original cross, the population from self-pollination would be practically all homozygous by the tenth generation. The population would then be expected to contain a number of different homozygous types. It might be anticipated that the weaker of such types would fail in the struggle for existence. But if we examine the facts, we find that *Œ. biennis* in Holland is remarkably uniform and has always been so, never showing any variations on the dunes except the *sulfurea* mutation, and *leptomeres* with cruciate petals. There is thus a complete absence of data on which to found a hypothesis of hybridity, while the evidence to the contrary is strong.

Cat. under the name *Lysimachia corniculata non papposa, Virginiana major, flore sulphurea.*[1] It must then have been appearing as a mutation in the original stock brought from America. Other wild American self-pollinated species recently brought into cultivation have been shown to be doing the same thing, *i.e.*, producing mutations with varying frequency. We must recognize that the germ-plasm of a species is a vast aggregation of units, among which complicated relationships arise which express themselves in throwing off at intervals new forms.

The frequency with which the mutations in *Œ. biennis* appear has been studied by de Vries (1915b). He grew 8500 plants from the pure line of Stomps, derived from a single wild plant from which they were descended in the third and fourth generation. They included 8 dwarfs (mut. *nanella*) or 0·1%, and dwarfs also occurred in later generations. The population of 8500 also contained 4 *semigigas*, or 0·05%,[2] and 27 *sulfurea*, or 0·3%. The latter appeared among the offspring of all seven parent plants. This gives a total of 39 mutations, or 0·45%. This is a lower percentage than in *Œ. Lamarckiana*, but much higher than in Drosophila. Cultures of *Œ. biennis sulfurea* from four of Stomps' mutants also gave two dwarfs among over 1000 plants which flowered. These give the race *Œ. biennis* mut. (1913) *sulfurea* mut. (1914) *nanella*. In this connection de Vries also obtained two other mutations from crosses. *Œ. lamarckiana* × *Œ. biennis nanella* yielded 55 plants, which had the characters of *lamarckiana* × *biennis*, except one *lata* mutant. Again, in the cross *Œ. biennis semigigas* × *Œ. biennis*, he obtained 19 plants, 1 dwarf mutant, 10 *biennis* with 14 chromosomes, and 8 of a new type (described elsewhere) with 15 chromosomes. The appearance of two uniform types in this cross is significant, for it shows that the meiotic processes were taking place so as to reduce the chromosome number in the gametes to 7 or 8. Moreover the fact that the 15-chromosome type was uniform indicates that the same chromosome must have been the extra one in every case.

This brings us to the meaning to be attached to the term parallel in connection with mutations. It is obvious that each mutation of a given type is parallel to every other of that type.

[1] See *Mutation Factor*, pp. 66, 158. The fact that the early writers, although they recognized *sulfurea*, found no other variations of *Œ. biennis*, shows that it was as uniform then as it is now.

[2] If mut. *gigas*, appeared only from the union of two diploid gametes, its frequency should then be about 1 : 4,000,000.

For example, each time *lata* appears as a mutation from *lamarckiana* the change involved must be the same. Again, in the sense in which the term originated, *Œ. biennsis lata*, *lamarckiana lata* and *suaveolens lata* are all parallel forms. Going farther afield the *cruciata* forms from *lamarckiana* and *biennis*, if independent in origin, are obviously parallel, but a number of wild species (shortly to be considered) which are unrelated to each other have cruciate flowers as a specific character. Some of these may have a common descent from a cruciate ancestor, others have almost certainly originated independently as parallel mutations. Nor is it certain that the change involved is always the same. The Drosophila work has shown that two mutations may be so closely alike as to be scarcely distinguishable, and yet have different relations in the germ-plasm.

The conception of parallelism is perhaps even more fertile when applied to the comparison of variations in different genera. A cruciate mutation has appeared in *Epilobium* and a similar variation probably occurs in other genera. Again, the phenomenon of doubling in flowers, to be considered later, shows that doubling may occur as parallel mutations in wild as well as cultivated species of many families. The same of course is true of white varieties, which almost any species of flowering plant may produce. Laciniation of leaves, maximum anthocyanin development, nanism, lack of chlorophyll (though such a condition may arise from various genetic causes), doubling, and a number of other characters may be looked upon as probably at any rate parallel mutations. Thus *Œ. rubricalyx* and the copper beech may be parallel in that they involve in their origin the same kind of germinal change. But this cannot be assumed with safety until it has been proved by breeding experiments with each. Thus some forms of flower-doubling are dominant and some recessive, and white varieties may originate in a number of ways. The same is true of gigantism. The *gigas* mutations from four species of Œnothera (Table II) show exactly the same peculiarities of stoutness, increase of cell size, 4-angled pollen grains and tetraploid chromosomes, so that the change is obviously the same in all cases. But in other genera gigantism may occur with or without tetraploidy. This whole subject will be considered further in connection with the variations of wild species of plants and animals.

The cruciate character.

Coming now to the *cruciata* type of mutation,[1] *Œ. biennis* var. *leptomeres* of the Holland sand dunes differs from the species in having narrow, linear petals, somewhat crumpled and more or less greenish yellow. This constant form Stomps (1913) regards as a case of incomplete sepalody, in which the petals have become imperfectly transformed into sepals. In *Epilobium* he describes a somewhat different form, *E. hirsutum cruciatum* de V., which originated from a group of a dozen plants (perhaps derived by stolons from one) and breeds true. The plants were found by Mr. John Rasor in Woolpit, Bury St. Edmunds, and seeds were sent to de Vries. They differ from the type in having, in place of the large, obcordate, lilac petals, small greenish scales shorter than the sepals, and pointed. That this is not a case of arrested development is shown by examining the young buds of the species. The petals are broad and obcordate even while still small and colourless. The buds of the cruciate form show also a tendency to dry up and fall when young. This appears to be a more complete case of sepalody. Crosses between type and variety gave a Mendelian ratio. Thus *E. hirsutum cruciatum* × *E. hirsutum* gave an F_2 of 323 plants, of which 245 were type and 78 variety. Also the reciprocal cross produced 177 plants in F_2, 130 of which were type and 46 variety, while one failed to flower. The sum of the two ratios is 375 : 124, showing that the *cruciata* mutation is a simple Mendelian recessive character.

Not only does the cruciate mutation from *Œ. biennis* differ from that of *E. hirsutum* externally, but also in its hereditary behaviour. For in reciprocal crosses of *Œ. biennis cruciata* with the parent type, while the F_1 is normal and the F_2 splits into the two original forms, yet the ratios are not Mendelian. Stomps unfortunately gives no figures, but states that whichever form is used as the male parent, that form appears in the greater number of the F_2 progeny. The cruciate forms in these two genera, while comparable in general, are not therefore strictly parallel forms.

Elsewhere (1913a, p. 25) the writer has shown that, whatever the origin of *Œ. lamarckiana* var. *cruciata*, both normal and cruciate flowers may occur on the same plant. This somatic

[1] See also *Mutation Factor*, p. 21. In addition to the specimen collected by Ernst de Vries, others have been found on the Lüneburg Heath, and they have been reported from other parts of Holland, probably from independent mutations.

segregation is apparently the same type of behaviour as was found[1] in the F_2 and F_3 of crosses between the large-flowered *Œ. rubricalyx* and the small-flowered *Œ. biennis*, in which large and small flowers frequently appeared on the same plant, and even long and short petals, of varying lengths, on the same flower. It is possible that this race of *Œ. lamarckiana* var. *cruciata*, which emanated from the Bremen Botanic Garden, may have originated by a cross between *Œ. biennis leptomeres* and *Œ. lamarckiana*. This hypothesis is supported by the short style in the flowers of this race, so short that, like *Œ. biennis*, nearly all the flowers were self-pollinated. But in crosses between *Œ. biennis* and its cruciate mutation there are no reports of this vegetative segregation, with both types of flowers on the same plant.

As a result especially of the studies of MacDougal (1905) and Bartlett (1914a), a number of cruciate species and varieties are now accurately known. As Bartlett points out, it is clear that these have not had a common origin, but they have arisen independently from different stocks, some more remotely and some more recently, just as var. *leptomeres* apparently originates even now from *Œ biennis* L. The first cruciate form to be discovered was *Œ. cruciata* Nutt. Its taxonomic history is given by Bartlett. Nuttall found it in Massachusetts and sent seeds of it to several botanists. Don grew it in 1824 and described it under Nuttall's name. The species which is still cultivated in botanical gardens under this name is quite likely descended from this original source. Its variable petals indicate that it has been crossed with a broad-petalled species, and it is now called *Œ. cruciata*, var. *varia*, de Vries.[2] In the sixth edition of Gray's Manual (1889) it was classed as probably a rare garden sport, since no specimens had been collected except in gardens, subsequent to the original collection over 60 years earlier. In later years cruciate specimens were collected in Vermont.

The interest awakened in wild North American Œnotheras by the work of de Vries, soon led to the discovery of other forms. Seeds of a cruciate form which had been collected at Sandy Hill, New York, near Lake George, in 1902, were divided, part of them being grown by MacDougal (1905) at New York, and a larger number by de Vries at Amsterdam. This material contained two

[1] See Gates, 1917a.

[2] De Vries found that this variety segregated roughly into three groups, (1) cruciate, (2) intermediate, (3) broad-petalled. The latter is constant except for rare cruciate bud mutations.

distinct types, one with rather broadly linear petals and rather thick flower-buds, the other with narrowly linear petals and slender flower-buds. A third cruciate type grown at Amsterdam in 1903, from seeds collected at Jaffrey, New Hampshire, differed in having a much longer calyx tube, and a more slender, less nutating stem. MacDougal (1905) gave descriptions of a third type from the Lake George seeds, which he identified with the New Hampshire form, but this identification is doubtful, as Bartlett points out. None of these three types is the same as *Œ. cruciata* Nutt. which came from Massachusetts. The two Lake George forms were described (Bartlett, 1914) as *Œ. atrovirens* Shull and Bartlett and *Œ. venosa* Shull and Bartlett. These may of course be cruciate varieties of the local species where they occur, but it seems more probable that they represent independent species. This would indicate that they have undergone further evolution since the cruciate mutation took place, or that the parent broad-petalled type has since become extinct.

Herbarium specimens with cruciate flowers, which have been placed under *Œ. cruciata* Nutt., but no doubt belong to several distinct types, have been recorded (Bartlett, 1914), from Nova Scotia (Sable Island), Maine, New Hampshire, Vermont, New York and Massachusetts. Another cruciate type with small flowers is represented by a specimen in the British Museum[1] collected in British Columbia in 1909—evidently an independent local variety or species. Bartlett also grew 50 plants from seeds of one individual collected at Springfield, Missouri. They were uniform with the exception of one plant, a single branch of which bore cruciate flowers. The petals were narrowly oblong, rather than linear. This suggests previous crossing with a cruciate mutant, which may very well have occurred in the field. Bartlett has cultivated a cruciate Œnothera from Mobile, Alabama, and describes another one, *Œ. stenomeres*, from Montgomery, Co. Maryland, which has given rise to mutations. Yet another cruciate species has been cultivated by Shull from Long Island, and has been described as *Œ. cleistantha* Shull and Bartl. (Bartlett, 1915e). It is not closely allied to any other known species, and the origin of the cruciate feature is therefore probably of ancient date. The flowers as a rule never open, and the most striking features of the species are its extreme leafiness and dense branching. It is obvious that the possibilities of natural crossing in this species are

[1] Gates, 1915a, p. 21.

very remote indeed. A minute but distinctive difference is in the large hairs of the calyx. On the bud-cone they are strongly ascending except around the top of the hypanthium where they are retrorse or perpendicular.

The cruciate form from Jaffrey, New Hampshire, is described by Bartlett, in the same paper, under the name *Œ. Robinsonii.* There is said to be "enough likeness between *Œ. venosa* and *Œ. Robinsonii*, so that a close relationship between them seems not unlikely." The differences from *venosa* are chiefly in the smaller size of *Robinsonii*, its more sharply dentate leaves, narrower bracts, longer more slender buds with dense erect viscid puberulence, and shorter calyx tips. The range of variation in bud length overlaps, however, and most of the differences are only obvious in the living plants. These two forms evidently represent closely allied elementary species rather than species in the Linnean sense. Both having cruciate flowers, one from New York State, and the other from New Hampshire, in the absence of local species of which they could be varieties the common character of cruciateness probably originated some time ago, and we may suppose that the series of small differences which distinguish the two species throughout have originated since.

Contrasted with these forms, in which the cruciate character appears to be of relatively ancient origin, is another cruciate species, *Œ. stenopetala* Bicknell, described from Nantucket Island in 1914. It is closely allied to the broad-petalled species *Œ. Oakesiana* Wats., from which it is probably descended. Yet the two have diverged in certain respects. In the case of *Œ. biennis leptomeres*, which apparently is still appearing as a mutation from *biennis* in Holland, the single difference in the flowers is unaccompanied by any other differences. This series is a most instructive one as a basis for contrasting the conspicuous unit difference of sudden and repeated origin, with the other smaller differences relating to all parts of the plant, by which the species have subsequently become differentiated. Whether the same type of evolutionary change is represented in both cases, is a matter worthy of close and prolonged study. By comparison and crossing of these cruciate forms, definite evidence might be obtained on this point. In many cases such elementary species differ from each other in physiological characters or methods of reaction to environment. An intensive study should make it possible to determine what relation if any these physiological and morphological differences bear to each other.

Cruciateness affords the most conspicuous and instructive examples of parallel mutations among wild Œnotheras. There are indications that the red hypanthium, which is the most conspicuous feature of the mutant *rubricalyx*, may also be paralleled, though in a less degree, by certain wild species. Thus *Œ. rubescens* Bartlett (1914b) has buds and hypanthia which are pale red. It would appear to agree in this feature with the form, probably hybrid in origin, which the writer[1] described from Lancashire under the name *Œ. rubrinervoides*. A small-flowered undescribed species, *Œ. columbiana*, from near Washington, is said by Bartlett to have "conspicuously red hypanthia." The writer has pointed out elsewhere[2] that the deep red of *rubricalyx* may become pale red by crossing and then back-crossing with a greenish-budded species. Thus in (*Œ. rubricalyx* × *grandiflora*) × *grandiflora*, if the female parent is heterozygous for the red factor, segregation into types with red or green hypanthia will take place, but the red will be much paler than in the selfed offspring of the female parent plant. In other words, the colour is diluted and the red remains permanently pale in the selfed offspring of such plants, deep red only being restored by a back-cross with *rubricalyx*. Red or reddish hypanthia in plants from all these different sources, indicate its appearance through independent variations in different species.

Parallel Mutations in Drosophila.

Various features of the Drosophila work will be discussed later. In *D. melanogaster* (*ampelophila*) certain mutations have occurred repeatedly. Thus (Morgan, 1919) white eyes have appeared independently three times, vermilion eyes at least six times, rudimentary wings five times, cut wing four times, truncate and notch wings each several times, but in the last two cases the change involved may not always have been the same.

In the last five years a number of mutations in six other species of Drosophila have been recorded. This includes a new eye-colour (scarlet) in *D. repleta* (Hyde, 1915a), another sex-linked mutation (light grey thorax) in the same species (Sturtevant, 1915), a wing mutation (jaunty C) in *D. confusa* (Hyde, 1915b), one in *D. tripunctata* (Metz and Metz, 1915), three mutations (extra bristles, triangle wing veins and short wing veins) in *D. obscura* Fall., and one (chocolate eye-colour) in *D. similis* Will. from Cuba (Metz, 1916b). In "species B," now known as *D. virilis* Stt., a more detailed study

[1] Gates, 1914b. [2] Gates, 1914a, 1915f.

of the mutations has been made. In four successive papers (Metz, 1916a, 1916b, 1918, 1920) a great many interesting facts have been recorded. *D. virilis* is known (Metz, 1914, 1916c, 1916d) to have six pairs of chromosomes, including one pair of small or m-chromosomes, whereas *D. melanogaster* has 4 pairs. In the latter species it has been shown that the 200 or more mutations all fall into the corresponding four groups. In *D. virilis* Metz (1920) has recently reported a total of 27 mutations, including 14 which are sex-linked (Group I), 3 in Group II, 4 in Group III, 3 in Group IV, and 3 in Group V. No mutations have yet been found corresponding to the small pair of chromosomes, but the late appearance of mutations from such small chromosomes is to be anticipated on the laws of chance, and the two known members of the corresponding group in *D. melanogaster* were not discovered until a very large number of mutations were known.

In an earlier paper (Metz, 1918) dealing with eight sex-linked characters in *D. virilis*, half of them were found to correspond closely to mutations of *D. melanogaster*. These four were yellow body-colour, magenta eye-colour, glazed eye-surface, and forked bristles on the thorax. The yellow mutation is slightly darker than in the case of *D. melanogaster*, but this is to be expected if the changes correspond, since the normal *virilis* is a darker species. In the forked mutation " the morphological correspondence is complete even to the smallest detail." Yellow and forked are not only sex-linked mutations, and hence in the X chromosomes, in both species, but their linkage relations are shown to be similar, so that they occupy corresponding positions in the X chromosome, yellow being terminal and forked about 55 units from it as measured by the percentage of crossing over. There are indications that the actual amount of crossing over is greater in *D. virilis*.

Confluent, referring to the veins on the wings, is another mutation which has its counterpart in *D. melanogaster*. It is a dominant, is not sex-linked, and when present in a homozygous condition has a lethal effect, as shown by the ratios of confluent in crosses and by the absence of homozygous individuals, though there is still a possibility that some may occur in *D. melanogaster*. Black body and morula-eye are other non-sex-linked mutations occurring in both species.

The six pairs of chromosomes in *D. virilis* have apparently been derived by transverse segmentation of two long boomerang-shaped pairs of chromosomes in *D. melanogaster*, the other two

pairs remaining unaltered. The evidence from those parallel mutations with similar linkage relationships shows that even the finer elements of the germ-plasm have maintained their relative positions and potentialities from species to species. This indicates a degree of static fixity combined with mutation in single elements which is truly remarkable, indicating that even the finer details of structure in the germ-plasm may maintain their spatial relationships for long periods. A number of the mutations in *D. virilis* have not appeared in *D. melanogaster*, though it does not follow that the latter species is incapable of producing them. At present it is quite unknown why one mutation rather than another appears at any given time, though the evidence is strong that each represents an actual transformation of a germinal element, and not merely a loss.

Clearly, the conception of parallel or homologous mutations is destined to be a very useful one in germinal analysis and in the study of relationships. In the next chapter we will consider its application to the study of variations in wild species.

LABORATORY NOTE.

NOTE ON AN IMPROVED METHOD FOR DEMONSTRATING THE ABSORPTION OF OXYGEN IN RESPIRATION.

I HAVE for some time been dissatisfied with the method which, I believe, is most generally employed in lectures and practical classes for demonstrating the fact that germinating seeds remove oxygen from the air by the process of respiration.

The apparatus, as figured in Darwin and Acton's "Physiology of Plants" (Fig. 15) or in Keeble's "Practical Plant Physiology," consists of a filtering flask fitted with a cork and containing germinating seeds and a test-tube with strong caustic potash solution to absorb the carbon dioxide produced. To the side tube of the filtering flask is attached a long vertical glass tube, the lower end of which dips into a dish containing mercury. The carbon dioxide produced by the respiring seeds is absorbed by the caustic potash, and that some oxygen is used up in the process is shown by the mercury rising in the vertical tube.

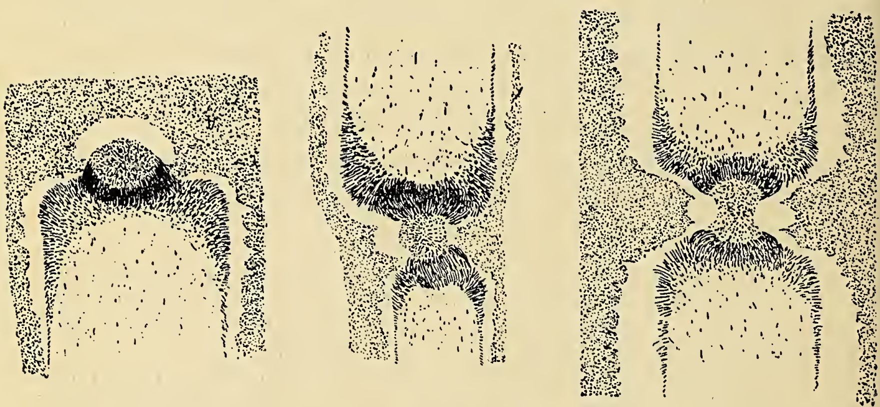
The objection to this form of apparatus is that the vertical column of mercury acts principally as a manometer registering a decrease in pressure, and the level of the mercury rises only a very few inches. So the fact that the germinating seeds are capable of using up in respiration all or nearly all of the oxygen in the flask, amounting approximately to one-fifth of the volume, is insufficiently demonstrated by the experiment.

I would suggest the slight modification in the apparatus shown in the accompanying figure, which, I think, requires but little explanation, as an improved method of performing the experiment. In practice it has been found to give good results.

The filtering flask containing some peas, which have been previously well soaked in water to start germination, rests on the table. The strong caustic potash solution is contained in a short wide specimen-tube, which is suspended by a loop of cotton from a bent pin stuck into the cork of the flask. The horizontal glass tube, connected with the side tube of the flask by a piece of indiarubber tubing, has its last inch or so bent at right angles, and dips into a dish nearly full of mercury supported on a wooden block.

The absorption of the oxygen by the germinating peas causes the mercury to be drawn into the tube, whence it runs into the flask and collects at the bottom, lifting up the seeds which float on its surface, thus showing clearly that a considerable amount of oxygen has been taken from the air contained in the flask during respiration.

The horizontal tube should slope very slightly upwards towards the flask to prevent any mercury running down into the flask by its own weight, and the level of the mercury in the dish should be kept only a little below the level of the side tube so that the mercury will require to be raised only a slight vertical distance.



If a graduated glass cylinder with a side tube could be substituted for the filtering flask, the apparatus might be employed for rough quantitative work. The objection to using an ordinary graduated glass cylinder and bending the proximal end of the mercury tube at a right angle so that it might pass through the cork closing the mouth of the cylinder, would be that the difference of level between the extremity of the tube inside the cylinder and the level of the mercury in the dish outside would cause this tube to act as a siphon when the mercury began to run into the cyliuder.

On the other hand, if one tried to avoid this happening by keeping the mercury in the dish at a slightly lower level than the opposite extremity of the tube, a negative pressure sufficient to affect seriously the result of a quantitive experiment would be required to raise the mercury in the tube.

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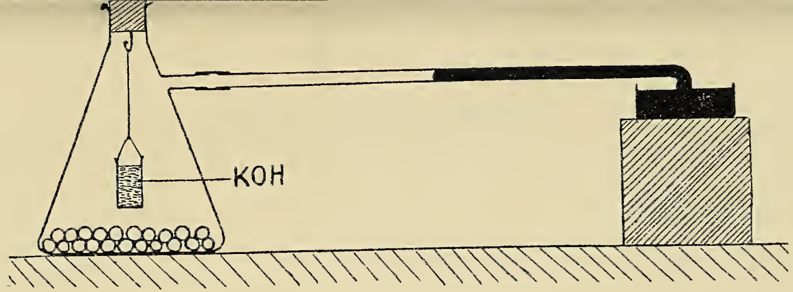
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HYBRIDISM AND CLASSIFICATION IN THE GENUS ROSA.

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IT is generally recognised by students of the British Flora that the genus Rosa presents interminable difficulties in connection with the classification of its innumerable forms into anything like a satisfactory or natural system. This fact, it seems to me, is reflected in the ever-increasing number of names which go to swell an already lengthy British Rose List. Scarcely a year passes which does not witness the publication of new "species" or "varieties" which are considered by their authors as deserving distinctive names because the plants show a few differences, very often only minor ones, from allied species.

Among the earlier workers we find that Baker (1869) in his *Monograph of British Roses* is content with thirteen species (eleven, if we omit *R. rubella* Sm. and *R. pomifera* Herrm. which are doubtfully native) and a moderate number of varieties. On the other hand, the London Catalogue of British Plants (1908) enumerates twenty-five native species and a large number of varieties, many of the additional "species," of course, being Baker's varieties, while in the List of British Roses by Wolley-Dod (1911) about one hundred and seventy names appear. Since this author expresses no opinion as to the relative value of the names, it is difficult to say how many are intended to stand as species.

There are probably no plants more variable than roses and it is perhaps not too much to say that no two bushes of the same "species" are quite alike in all the technical characters relied upon by rhodologists for making a diagnosis. In the case of many micro-species it is found on investigation that authentic specimens collected or named by the authors themselves neither agree with the original

descriptions nor with one another. If the creation of new names continues at the present rate and according to the present system or want of system, the time will soon arrive when it will be impossible to say more of any member of the genus than that it is a rose. To make a determination and to give a binomial will become the work of a few specialists and there need be little hesitation in predicting that no two specialists will agree.

There is, no doubt, a strong tendency to place an ever finer construction on the idea of species whenever a genus is submitted to critical investigation and it is contended by many that the Jordanian practice of splitting the "Linnean species" into innumerable forms or micro-species has, in many instances, been carried to an extreme. Whatever the advantages or disadvantages of this practice may be, it brings us face to face with the problem of deciding what forms are to be regarded as worthy of specific rank. On this question, in so far as it concerns the genus Rosa, a unanimous opinion is not likely to be forthcoming, for "species" of Rosa must, in the present state of our knowledge, rest largely on differences which are in themselves artificial, and the chief difficulty is to decide what are really important and what are unimportant differences. It is gradually being realised that external morphology alone is inadequate for the solution of such problems, yet it is remarkable that still very few "critical species" among British plants have been subjected to the test of experimental investigation. Only by culture, combined as far as possible with cytological study, will it become possible, I think, to determine finally the genetic relationships of the numerous micro-species into which old, well-known species like *R. canina* Linn. have been split.

Regarding purely morphological investigation, it may be of interest to refer here to the work of Parmentier (1898), who endeavoured to throw some light on the problem by following the anatomical method. This worker, after an exhaustive enquiry into the detailed structure of the plants, divided the genus into primary species, morphological species, morphological sub-species and secondary forms. But this does not appear to have produced a better or more natural classification than that adopted by systematists. We find, for example, that while *R. canina* L. ranks as a primary species, *R. lutetiana* Lém., *R. dumetorum* Thuill. and *R. coriifolia* Fr. belong to the third category and *R. glauca* Vill. is a mere secondary form. Whatever the value to be attached to these forms of the aggregate *R. canina*, systematic students are

generally agreed in holding *R. glauca* Vill. to be as good a "species" as *R. lutetiana* or *R. dumetorum*. A knowledge of the anatomical construction of plants is useful and often very helpful, but taken alone it is not always sufficient to solve the problems of relationship.

One of the most striking results of the intensive study of British plants is the increasing number of hybrids that are being recognised. One need only mention such genera as Viola, Epilobium, Mentha and Salix. The presence of hybrids renders the classification of such genera extremely difficult, and it is not improbable that the difficulty in classifying roses may be largely due to hybridisation and segregation, complicated, it may be, by re-hybridisation. When one considers the general prevalence of wild roses, the frequent association of numerous species and forms in the same habitat, the large numbers of flowers produced by fully developed plants, it becomes evident that there must be abundant opportunities for natural crossing.

Several hybrids, in the sense of crosses between distinct species, have been recognised among British Roses. The commonest is *R. involuta* described by Smith, *Fl. Brit.* 1804, from material collected in the West of Scotland. It was not until 1884, however, that its hybrid origin was suggested, when Christ promulgated the idea that *R. involuta* Sm. is a natural cross between *R. pimpinellifolia* and *R. tomentosa*. This view is now universally accepted. *R. involuta*, though not common, is fairly widely distributed in the North of England and in Scotland, and it may be expected to occur wherever the two parents grow together. Numerous forms of the hybrid are to be found and many of these had received varietal names before the hybrid nature of this rose was realised. While *R. pimpinellifolia* shows little or no variation, *R. tomentosa* is decidedly a polymorphic species and considerable variation in *R. involuta* need not, therefore, be unexpected. In general, the characters of the hybrids are more or less intermediate between the unlike characters of the two parents, but some of the forms bear a greater resemblance to one or to the other parent, and it is not impossible that this may be due to *R. pimpinellifolia* being the seed-parent sometimes and *R. tomentosa* at other times. The hybrid plants are usually vigorous, flower freely and are more or less sterile, thus showing some of the attributes of hybrids between distinct species. Whether these hybrid forms of *R. involuta* breed true or whether they segregate is unknown, but the work of Brainerd (1906) on Viola suggests the need for similar investigation in the case of our natural rose hybrids.

Again, *R. hibernica*, described by Templeton in *Trans. Dublin Soc.* III. 1803, from plants found in the North of Ireland, is now regarded by all rhodologists as a hybrid between *R. pimpinellifolia* and *R. canina* Linn. sp. agg., although this view was not generally accepted when first advanced by Christ in 1875. *R. hibernica* is a comparatively rare plant, being known from only a few vice-counties in the North of England and from a few in Scotland, besides its two stations in Ireland, and apparently only the glabrous variety has been found on the Continent. The typical plant has leaflets hairy at least on the nerves below which is sufficient evidence to show that the second parent is a *dumetorum* or a *coriifolia* form, probably the former if the sepals become reflexed, the latter if the sepals become erect. *R. hibernica* var. *glabra* Baker has glabrous leaflets, and possibly in this case the second parent is a form of *R. canina* or of *R. glauca*, both of which are without pubescence on the leaves. *R. hibernica*, like *R. involuta*, is almost universally sterile and the remarks made in the discussion of the latter apply equally to this hybrid.

R. pimpinellifolia hybridises also with *R. rubiginosa*, but the hybrid is extremely rare. The British forms, the first of which was recognised as recently as 1896, have not received a binomial, but they are not markedly different from the French forms of the hybrid known as *R. biturigensis* Bor. The hybrid is most abundant on the coast of Haddington, where it grows in association with both parents. It is remarkably luxuriant, some of the bushes attaining a height of eight or nine feet. The plants are not so obviously sterile as the majority of *R. involuta* and *R. hibernica* forms, and two distinct types are recognisable in the shape of the fruit. In one the fruit is ovoid or oblong, recalling that of *R. rubiginosa*, in the other it is globose and therefore similar to that of *R. pimpinellifolia*.

A hybrid of *R. pimpinellifolia* and *R. mollis* has been recorded from several vice-counties in Scotland, the first record being based on the determination of specimens from Sutherland by Crépin. Similar plants have been discovered in Banffshire and in Perthshire and in all cases the evidence tends to point to *R. mollis* as the second parent. In addition the following hybrids, which do not involve *R. pimpinellifolia*, are recorded by Wolley-Dod (1911)—*R. arvensis* Huds. × *stylosa* Desv., *R. suberecta* Ley. × *mollis* Sm. and *R. suberecta* Ley × *coriifolia* Fr. In the absence of experiment it is impossible to confirm or contradict these determinations. The first two hybrids must be uncommonly

difficult to diagnose as such, since the supposed parents are so closely similar in many features. There is nothing improbable, however, in the supposition that closely allied species may hybridise just as freely as the species mentioned in the foregoing paragraphs. This theoretical consideration is of great importance and it bears very directly on the whole discussion which follows. If closely related species or species and varieties hybridise the hybrid origin of the offspring would be exceedingly difficult to detect. In actual practice they would not, as a rule, be distinguished as hybrids, but would be considered distinct species or varieties and would be named as such. Thus, perhaps, has arisen a large portion of the total number of named varieties of roses. It is exceedingly interesting to find, therefore, that Almquist, one of the most recent writers on the genus, treats *R. glauca* and *R. coriifolia*, two very closely related forms, as a collective species under the name *R. Afzeliana* Fr.= *R. glauca* × *coriifolia* (see Traaen, 1913).

On the general question of hybridism in the Rosaceæ the work of Jeffrey may be mentioned. "Not only are certain of the Rosaceæ recognisable as hybrids on account of their transitional features of organisation, Mendelian phenomena, etc., but certain others which have not revealed themselves as hybrids in these ways are clearly such as a result of a study of their spores. We have consequently to distinguish in the case of the Rosaceæ, if the morphological features are taken into account as well as the data of systematic botany, three kinds of individuals, namely, pure species, recognised species which from the condition of their pollen are in reality concealed hybrids or crypthybrids, and recognised hybrids." The subject, in so far as it concerns the genus Rosa, has been pursued by Miss Cole (1917) who, from a study of the pollen in numerous roses, concludes that the genus contains only a few pure species, while the great majority of so-called species are really of hybrid origin. Unfortunately, Miss Cole's investigation does not include many species native in Britain, and the condition of the pollen in British forms I hope to make the subject of a future paper.

It has already been mentioned that there is no experimental evidence to show whether the species-hybrids described above segregate or remain stable. It has generally been believed that only crosses between varieties segregate, but the work of Brainerd (1907) on American Violets points clearly to segregation in the offspring of species-hybrids. Brainerd found growing wild

numerous violets which he determined as natural hybrids between certain species. These plants were taken into cultivation and found to be more or less sterile, but the small number of seeds obtained from cleistogamic flowers gave rise to plants showing segregation in regard to several features. "It is certain," according to Bateson, "that segregation in countless instances plays a part in the constitution and maintenance of characters held by systematists to be diagnostic of species. One has only to glance over trays of birds' skins, the portfolios of a herbarium, or drawers of butterflies and moths to discover abundant 'species' which are analytical varieties of others. The principles of heredity we trace in our experimental breeding are operating throughout the natural world of species."

If segregation occurs in the genus Rosa, and it is difficult to believe that it does not occur, we might expect to find a large number of visually distinct forms showing various combinations of Mendelian unit characters such as hairiness, leaf serration, glandularity, glaucousness, etc. Moss (1912) has pointed out that the numerous forms of the highly variable species *Stellaria dilleniana* Moench. may be regarded theoretically as various combinations of several unit characters such as glaucousness or greenness, large or small petals and many-flowered or few-flowered cymes.

Before attempting to make a theoretical analysis of some of the British species of Rosa on the basis of a few separate characters such as have been mentioned, it will be useful first to indicate the groups into which the genus may be divided. For this purpose the following table, which presents the sections and groups more or less in accordance with the views generally held by systematists, has been drawn up.

It will be seen from the dates of publication included in brackets in Table I that the term "group" generally, though not always, corresponds to one of the older aggregate species. The numerous sub-species and varieties of these aggregates which have since been described I shall attempt to analyse as far as is possible on the basis of a few characters commonly employed by systematists for the differentiation of these forms.

Rosa arvensis Hudson, *Fl. Angl.* 1762, is the British representative aggregate species of the Section Synstylæ in which the styles are combined into a long slender column equalling the stamens. A number of forms (the term is used throughout in a

TABLE I.

Section I. SYNSTYLÆ.

Group of *Rosa arvensis* Huds. (1762).

Section II. STYLOSÆ.

Group of *Rosa stylosa* Desv. (1809).

Section III. CANINÆ.

Sub-sect. Eu-caninæ.

Group of *Rosa canina* Linn. (1753).

" " *dumetorum* Thuill. (1799).

" " *glauca* Vill. (1809).

" " *coriifolia* Fries (1814).

" " *subcanina* Chr. (1873).

" " *subcollina* Chr. (1873).

" " *tomentella* Lém. (1818).

Subsect. Rubiginosæ.

Group of *Rosa Eglanteria* Linn. (1753).

" " *micrantha* Sm. (1812).

" " *agrestis* Savi (1798).

Subsect. Villosæ.

Group of *Rosa villosa* Linn. (1753).

" " *tomentosa* Sm. (1800).

Section IV. PIMPINELLIFOLIÆ.

Group of *Rosa pimpinellifolia* Linn. (1753).

Section V. PIMPINELLIFOLIÆ HYBRIDÆ.

Group of *Rosa involuta* Sm.

(*R. pimpinellifolia* agg. × *tomentosa* agg.)

Group of *Rosa hibernica* Templ.

(*R. pimpinellifolia* agg. × *Eu-caninæ*).

Group of *R. biturigensis* Bor.

(*R. pimpinellifolia* agg. × *rubiginosa* agg.)

general sense only) may be distinguished according to leaf-serration and the nature of the peduncles. To take these two characters only, (1) Biserrate leaflets (B), not biserrate (b), (2) Hispid, glandular or setose peduncles (S), smooth peduncles (s), the following four theoretical combinations may be expected—BS, Bs, bS, and bs. *R. arvensis* Huds. is a bS form and the smooth peduncled form bs is *R. erronea* Rip. The combination BS corresponds to var. *biserrata* Crép. This analysis does not include *R. ovata* Lej. which is simply a narrow-fruited variety of the type, nor *R. gallicoides* Déségl. a fairly well-marked form owing to the admixture of acicles on the upper part of the stems, a feature which

may possibly indicate that *R. pimpinellifolia* may have entered into the plant's composition through hybridisation. By some authors *R. gallicoides* is regarded as *R. arvensis* × *gallica*.

Rosa stylosa Desv. in *Journ. de Bot.* 1809, is the only aggregate species of the Stylosæ section, a group which is unquestionably intermediate in its general features between the Synstylæ and the Eu-caninæ, some authors including it in the former section while others place it in the latter. This intermediate position immediately suggests hybridisation between Synstylæ and Eu-caninæ forms in the production of those forms which constitute the Stylosæ. The distribution of *R. stylosa* agg. is the same as that of *R. arvensis* agg., while Eu-caninæ forms of the group *dumetorum* are widespread and it is from this group of the Eu-caninæ that some members of *R. stylosa* are almost indistinguishable. It might be interesting and instructive, therefore, to cross systematically *R. arvensis* and *R. dumetorum*.

In *R. stylosa* there is little variation in the serration of the leaflets, all the British forms being uniserrate except var. *evanida* Chr. which is biserrate. But the leaflets in some are hairy (H), in others glabrous (h). Forms with rose-coloured (R), others with white (r) flowers occur, while some have setose (S), others smooth (s) peduncles. If we deal with those three characters only, the following eight combinations would be visibly different—HRS, HrS, HRs, Hrs, hRS, hrS, hRs and hrs. At least five of these combinations have been met with in Britain and are known by distinctive names. The type of *R. stylosa* Desv. is the form HrS, while HRS corresponds to *R. systyla* Bast. Hrs is *R. stylosa* var. *corymbosa* Desv. = var. *opaca* Bak. and var. *pseudo-rusticana* Crép. is the combination hrS. *R. virginea* Rip. comes under the hrs combination. Only one form with rose-coloured flowers is included in this analysis, but another, viz. *R. parvula* Sauz. et Maill. occurs on the Continent and has been reported as occurring in Britain. It corresponds to the combination HRs.

We pass now to Section III which is a very large one, the subsection Eu-caninæ itself containing by far the largest number of our British species and varieties. In general, the members of this subsection can be distinguished by their large size and arching habit, their uniform and decidedly hooked prickles and by the styles being free, at least not agglutinated into a column like those of Synstylæ and Stylosæ. Since the division into groups given in Table I is not that most usually adopted by systematists

a few notes on the arrangement may be useful. The group *canina* includes that large assemblage of forms characterised by the possession of glabrous leaflets, glabrous or slightly hispid styles, late-ripening fruit and reflexed sepals which disarticulate before the fruit changes colour. The group *dumetorum* is the exact counterpart of *canina* except that its leaflets are more or less pubescent. Its numerous forms may be grouped together as an aggregate species, *R. dumetorum* Thuill. or they may be regarded simply as hairy-leaved varieties of *R. canina.*

R. glauca Vill. and *R. coriifolia* Fr. are distinct and clearly defined from *R. canina* and *R. dumetorum.* Their members develop ascending or erect sepals which are subpersistent, not falling until the ripening of the fruit. Moreover, the fruit ripens earlier than in *canina* or in *dumetorum.* The styles, which are never much exserted, form a dense hemispherical mass, strongly hispid or woolly, a character by which it is nearly always possible to distinguish members of *R. glauca* and *R. coriifolia* from those of *R. canina* and *R. dumetorum.* *R. glauca* comprises glabrous forms; in *R. coriifolia* the leaflets are hairy. I regard the four groups as constituting two sets of parallel series of forms. The first two are generally distributed throughout Britain while the third and fourth are confined to the north of England and to Scotland.

The four groups have been fairly fully worked out systematically and a large number of forms have been described and named. No attempt will be made to give an exhaustive analysis of all these forms based on many characters, but in Table II the primary divisions of the groups are shown and it will be seen that the characters used are the serration of the leaflets, the presence or absence of subfoliar glands, the development or non-development of hispid peduncles. To these must be added, of course, the pubescence of the leaves as the distinguishing feature of *R. dumetorum* and *R. coriifolia* from *R. canina* and *R. glauca* respectively. The primary divisions of the four groups have been named in the table as if they corresponded to species, and while this is true for some, it has to be mentioned that others were described by their authors as varieties only. It is clear, however, that if the four groups are treated as equal in value, all the names which correspond to parallel divisions of the groups should also rank equally; whether we call them species or varieties is a matter of individual opinion.

TABLE II.

Group.	*R. canina.*	*R. dumetorum.*	*R. glauca.*	*R. coriifolia.*
Leaflets uniserrate				
Peduncles smooth	*R. lutetiana* Lém. ...	*R. urbica* Lém.... ...	*R. Reuteri* God. ...	*R. incana* Kit. ... ...
,, hispid...	*R. andegavensis* Bast....	*R. Deseglisei* Bor. ...	*R. transiens* Gren. ...	*R. bovernieriana* Lagg. et Pug.
Leaflets biserrate				
Eglandular beneath				
Peduncles smooth	*R. dumalis* Bechst. ...	*R. arvatica* Bak. p.p....	*R. subcristata* Bak. ...	*R. Watsoni* Bak. ... ...
,, hispid...	*R. verticillacantha* Mér.	*R. aciculata* Rouy. ...	*R. fugax* Gren. ...	*R. cæsia* Sm. ... ...
Glandular beneath ...				
Peduncles smooth	*R. scabrata* Crép. ...	... ...	*R. stephanocarpa* Rip. ...	*R. Lintoni* Scheutz. ... ...
,, hispid...	*R. Blondæana* Rip. ...	... ...	*R. œnensis* Kell. ...	*R. Bakeri* Déségl. ... ...

If we make an analysis on the basis of (1) hairiness of the leaflets (H), glabrousness (h), (2) biserration (B), not biserrate (b), (3) the presence of glands on the leaflets (G), the absence of foliar glands (g), (4) hispid peduncles (S) and smooth peduncles (s), then there are sixteen theoretical combinations to consider:—HBGS, HBGs, HBgS, HBgs, HbGS, HbGs, HbgS, Hbgs, hBGS, hBGs, hBgS, hBgs, hbGS, hbGs, hbgS, and hbgs. We may apply these combinations first to the *canina-dumetorum* groups; the last eight containing h will be glabrous and thus correspond to *canina* forms. Six of the eight combinations have been named. *R. lutetiana* Lém. is the form hbgs,, and *R. andegavensis* Bast. corresponds to the hbgS form. The combination hBgs covers *R. dumalis* Bechst., while similar plants with hispid peduncles come under the hBgS form, known as *R. verticillacantha* Mér. The two biserrate "species" with subfoliar glands are *R. scabrata* Crép. and *R. Blondæana* Rip., the former with smooth peduncles, *i.e.* hBGs, the latter with hispid peduncles, *i.e.* hBGS. The combinations hbGS and hbGs are without names. Four of the eight combinations containing H have been met with in Britain and comprise the series of forms which are classified under the *dumetorum* group since the leaves are hairy. The Hbgs form corresponds to *R. urbica* Lém., and to the HbgS combination the name *R. Deseglisei* Bor. applies. Of the biserrate hairy forms, *R. arvatica* Bak. p.p. corresponds to HBgs, while the HBgS combination is referable to *R. canina* var. *aciculata* Rouy. Four forms having subfoliar glands, HBGS, HBGs, HbGS and HbGs, are so far not recorded. It will be seen, therefore, that of the sixteen theoretical combinations of the four selected separate characters ten have been named, six of them falling under the *canina* group, the remaining four being *dumetorum* forms. These ten names do not exhaust the list of British roses which are classified under the *canina-dumetorum* series. Under *R. lutetiana*, for example, nearly a dozen named forms which may be distinguished according to size and colour of leaflet, shape of fruit, etc. are mentioned in Wolley-Dod's "List." It is not improbable that these are important characters, perhaps more important than the presence or absence of glands on the leaves or peduncles, but the data regarding them is so incomplete for so many named varieties that it has been impossible to include them in the present analysis. In any case, the employment of more than a few unit characters would lead to unnecessary complications.

We may pass now to the *glauca-coriifolia* groups and proceed to an analysis precisely similar to that which has been applied to the *canina-dumetorum* series. If we take first the eight combinations which include h, *viz.* hBGS, hBGs, hBgS, hBgs, hbGS, hbGs, hbgS and hbgs, we shall be dealing with *glauca* forms. The combination hbgs is *R. Reuteri* God. and the hispid-peduncled form hbgS is *R. Reuteri* var. *transiens* Gren. *R. subcristata* Bak. is the form hBgs and *R. fugax* Gren. corresponds to hBgS. The biserrate forms with subfoliar glands are hBGs and hBGS, the former combination having been named *R. stephanocarpa* Déségl. et Rip., the latter being *R. glauca* var *œnensis* Kell. Only two of the eight combinations remain unrecognised, namely hbGS and hbGs. Turning now to the eight combinations having H in their composition, *viz.* HBGS, HBGs, HBgS, HBgs, HbGS, HbGs, HbgS and Hbgs, we find that six have been named. These, of course, come under the *coriifolia* group. *R. incana* Kit. is an Hbgs form and constituted the type of Fries. The combination HbgS is *R. bovernieriana* Lagg. et Pug. *R. Watsoni* Bak. and *R. caesia* Sm. correspond to the forms HBgs and HBgS respectively. The combination HBGs applies to *R. coriifolia* var. *Lintoni* Scheutz and the counterpart with glandular peduncles, HBGS, is *R. Bakeri* Déségl. Thus, in the *glauca-coriifolia* groups, twelve of the sixteen theoretical combinations have been discovered and have received distinctive names. Unfortunately, an analysis on the basis of glaucousness and non-glaucousness or greenness cannot be attempted since the distribution of these characters in all the forms of the two groups is not known. But these characters are unquestionably important ones, and they receive much emphasis in Almquist's classification of Swedish roses to which reference will be made later.

The names *R. subcanina* and *R. subcollina* date from 1873 when they were used by Christ in *Rosen der Schweiz*, the former to describe a variety of *R. Reuteri* (glauca), the latter as a variety of *R. coriifolia*. By some authors they are still regarded as varieties or sub-species, but there are certain advantages in treating them as independent groups equal in value, from the point of view of the systematist, to *R. glauca* and to *R. coriifolia*. Already, evidence is accumulating to show that they probably each comprise a series of forms developing along lines parallel to those dealt with for the two aggregate species of which they were respectively described as varieties. The type of *R. subcanina* (Chr.) is a uniserrate form, but

a biserrate form, *R. glauca* var. *denticulata* Kell., has been recognised. *R. subcollina* (Chr.), as at present understood in this country, is a slightly larger group, and includes the type of Christ, which is uniserrate, and at least three biserrate forms, *viz. R. subcoriifolia* Barclay, *R. cæsia* var. *incana* Bor. and *R. pruinosa* Bak. It would be possible to make an analysis of the *subcanina-subcollina* series on the lines already followed for preceding groups, though a considerable number of combinations would stand without names. But since the groups have not been at all fully worked out, it does not follow that the combinatious do not occur in nature. *R. subcoriifolia* Barclay is in itself a somewhat aggregate species. Its commonest form has subfoliar glands and smooth peduncles, and is thus an HBGs form, corresponding to var. *Lintoni* of the *coriifolia* group. But HBgs and HBGS combinations have also been met with, although they have not received distinctive names.

I have, however, a suggestion to make regarding the *subcanina-subcollina* series. *R. subcanina* is, in a number of features, intermediate between *R. glauca* and *R. canina.* Christ, in his description of the plant, remarks that it connects the two. In the possession of reflexed or downwardly spreading sepals it comes near *R. canina*, but in the woolly head of styles it bears a closer resemblance to *R. glauca.* In the length of the peduncles, the time of ripening of the fruit, and the persistence of the sepals it is more or less intermediate between *R. glauca* and *R. canina* and one is tempted to ask if *R. subcanina* may not be a hybrid between these two species. Again, *R. subcollina* as an aggregate is more or less intermediate in its characters between *R. coriifolia* and *R. dumetorum.* It holds an essentially similar position between these two aggregate species as *R. subcanina* does for *glauca* and *canina*, and one wonders if it, also, is not of hybrid origin. Experimental work is here extremely desirable. So far, as I am aware, there is nothing in the geographical distribution of these forms against the theory here suggested. Both *R. subcanina* and *R. subcollina* are most frequent in Scotland, becoming much rarer in the north of England, and they are quite absent in the south. Their distribution thus follows very closely that of *glauca* and *coriifolia.* *R. canina* and *R. dumetorum*, are, of course, abundant and widespread. It is noteworthy, also, that the two suggested hybrids, while they have the same distribution as *R. glauca* and *R. coriifolia*, are rarer than either of these two species.

There remains the group *R. tomentella* Lém. of the subsection Eu-caninæ. This is a small group, but a somewhat difficult one to segregate. Typical examples, possessing sub-orbicular, pubescent leaflets, more or less glandular beneath, and hard late-ripening fruit with reflexed sepals, are fairly easily recognised, but " some individuals," to quote Wolley-Dod, " are liable to be mistaken for members of *Tomentosa.* Its more glandular members also run near forms of *Micrantha* while those with eglandular leaflets are often very difficult to distinguish from the group *Dumetorum.*" The limits of the group are thus extremely ill-defined and it is not improbable that some of its members owe their indefiniteness to hybridisation with forms belonging to other groups. We may, however, attempt an analysis on the basis of leaf-serration (Bb), glandular or eglandular leaflets (Gg) and hispid or smooth peduncles (Ss). The following eight possible combinations have therefore to be considered: – BGS, BGs, BgS, Bgs, bGS, bGs, bgS and bgs. The type of *R. tomentella* Lém. is a BGs form, the variety with hispid peduncles, BGS, being var. *decipiens* Dum. An eglandular variety, the combination Bgs, may be placed, according to Wolley-Dod, in *R. carionii* Déségl. et Gill. although Déséglise himself regarded this as a *dumetorum* form. Of uniserrate forms, *R. obtusifolia* Desv. corresponds to the combination bGs, and the only other uniserrate member is *R. canina* var. *concinna* Bak. which closely resembles *R. obtusifolia*, but having hispid peduncles, it represents the combination bGS. Three of the eight combinations have not been named, BgS, bgS and bgs. If they did occur in nature they would be extremely difficult to distinguish from members of the group *dumetorum* since they are all eglandular forms.

We now pass to the subsection Rubiginosæ, the members of which can be distinguished from those of the Eu-caninæ primarily by the abundance of subfoliar scented glands. The subsection includes three groups which may be named after the aggregate species *Eglanteria* L., *micrantha* Sm. and *agrestis* Savi.

Comparatively small, more or less tufted plants, are characteristic of the group *Eglanteria.* The stems show small acicles mixed with the main prickles, which are hooked and curiously uncinate in shape, quite different from the type of prickle generally seen in Eu-caninæ forms. Whether this mixed armature is any indication of hybridity in the group as it certainly is in the case of *R. involuta* and *R. hibernica*, I am unable to say, but it is of considerable interest to note that Miss Cole found only 10% fertile

pollen in *R. rubiginosa* (*R. Eglanteria*), this remarkable pollen-sterility being attributed to hybridisation. All the British forms of *R. Eglanteria*, except *var. jenensis* Schulze, have strongly hispid peduncles, and are usually differentiated according to whether the main prickles are distinct from or gradually merge into the acicles and by the ultimate direction and relative persistence of the sepals. All these varying features may be the result of various crossings, although I am at present quite unable to suggest a possible parentage for the aggregate *R. Eglanteria.*

The members of the small group *micrantha* show a taller and more arching habit recalling that of *R. canina* L. The stems do not present any admixture of acicles with the main prickles. The peduncles are glandular hispid in all the British forms except var. *Briggsii* Bak. *R. Hystrix* Bak. may be distinguished from the type and from *var. permixta* Déségl. by its smaller leaflets, while the type may be distinguished from the last-mentioned form by the absence of prickles from the flowering branches.

The group of *R. agrestis* is also a small one and runs very close to that of *R. micrantha*, its members differing primarily in having smooth peduncles. They are small leafleted forms and it does not appear possible to segregate them satisfactorily, except perhaps on the basis of leaf pubescence, the presence of which marks off *R. sepium*, var. *pubescens* Rouy from the type of *R. agrestis* (=*R. sepium* Thuill.) which has glabrous leaflets.

The sub-section Villosæ may be regarded as comprising two groups only, one corresponding to *R. villosa*, L. of which *R. mollis* Sm. is the representative species in Britain, the other group being known under the name of *R. tomentosa* Sm. The members of the two groups vary considerably in habit, from low erect bushes to large, arching forms. The prickles are uniform, slender as a rule, straight or somewhat falcate. The leaflets are biserrate, very hairy, often softly tomentose and generally glandular, often decidedly so as in Rubiginosæ forms, but the glands have a resinous not a fragrant odour.

R. mollis Sm. is a tolerably well-defined species, at least as an aggregate, reaching its greatest frequency in the North of Britain. It varies chiefly in the amount of glandular development of the leaves and in the hispidity of the peduncles. To take these two characters only, we find that all the four theoretical combinations have been recognised, GS, Gs, gS, and gs, three of them having been named. The form gS, may be regarded as the type of *R.*

mollis Sm. while the combination gs, applies to the var. *cærulea* Woods. The GS form is *R. pseudo-rubiginosa* Lej. This leaves the combination Gs unnamed, but such forms are not unknown and have been frequently noticed occurring with the other varieties.

The group *tomentosa* is a more difficult one to deal with. It is usual, in this country at least, to divide it into three sub-groups according to the direction and relative persistence of the sepals. In *R. omissa* Déségl. the sepals ultimately become quite erect and persist until the fruit is ripe. On the other hand, the third sub-group, represented by *R. scabriuscula* Sm., includes those forms characterised by the possession of reflexed and early-deciduous sepals. An intermediate sub-group is that of *R. subglobosa* Sm.=*R. Sherardi* Davies, in which the sepals are spreading or no more than slightly ascending and they disarticulate before the fruit is fully ripe. The whole group is perhaps the most difficult one we have to classify and it would not be surprising to find that this difficulty is largely due to hybridisation and re-hybridisation among the different forms. An experimental investigation to discover whether *R. subglobosa* Sm. is not, in fact, a hybrid between *R. omissa* Déségl. and *R. scabriuscula* Sm. would be exceedingly valuable.

We come, finally, to the section Pimpinellifoliæ containing *R. pimpinellifolia* L. which is one of the best-defined and perhaps least variable species we have. Essentially a plant of sandy sea-coasts, it is nevertheless not unknown from inland stations. Its habit, setigerous stems, and distinctive foliage are features which at once distinguish it from other members of the genus. If we consider leaf serration and the nature of the peduncles, using the same letters as before, then, of the four combinations, BS, Bs, bS, and bs, the last-mentioned is the commonest form and applies to *R. pimpinellifolia*. The bS form corresponds to *R. spinosissima*. The only variety with fully biserrate leaflets is *R. Ripartii* Déségl. which corresponds to the combination Bs. In Britain this plant is somewhat rare, but a faint biserration is fairly frequently seen in the type. Well-defined forms of the BS combination have not been recognised, although forms approaching it have been recorded without any distinctive name.

In the theoretical analysis which has been attempted in the foregoing pages comparatively few characters have been taken into consideration. The selection of a few has been deliberate, as my main purpose has been rather to direct attention to the very high

probability of the presence of various combinations of Mendelian unit characters in the several groups than to give an extensive and involved analysis on the basis of a large number of separate characters. The argument throughout is, of course, entirely hypothetical and experimental results are required to establish the hypothesis. It is impossible to over-emphasise the need for cultural work, so intensive has the study of British plants become, and, as already pointed out, morphological methods alone are insufficient for the complete solution of the intricate problems involved. Yet, it is remarkable how little has been done to discover experimentally the genetic relationships within our numerous "critical species" and genera. The work of Trow (1912) on *Senecio vulgaris* Linn. clearly points to the need for similar studies on other aggregate species.

Almquist, whose work has already been mentioned, makes a very interesting attempt in his account of *Rosa*, in Lindman's *Svensk Fanerogamflora* (1918) to refer the micro-forms of the genus ultimately to certain characteristic types which are based on the following characters:—glaucousness, greenness, glabrousness and hairiness. "Species" with glaucous leaflets are referred to *gl.* (*glauca*) if they are glabrous, to *glf.* (*glauciformis*) if the leaflets are hairy. Green-leafleted "species" are referred to *vir.* (*virens*) if the leaflets are glabrous, to *virf.* (*virentiformis*) if hairy. This plan is applied throughout the eight sections and thirty-one species-types into which the genus has been divided. Thus, any rose whose sectional and type characters have been determined finds a place in Almquist's scheme according to whether it is a *gl.*, *glf.*, *vir.*, or *virf.* form. This method of segregation has involved the creation by Almquist of a large number of new names, especially in the Afzeliana *(R. glauca × coriifolia)* and Caninæ sections, where combinations of these characters are apparently frequent. But it is the scheme itself which claims one's attention and interest. Almquist contends that the chief characters in classifying roses are the colour and consistence of the leaves, the form of the leaflets and the shape and direction of the teeth. He pays little attention to the direction of the sepals, while biserration, the development of glands, etc., are regarded as modifications of primary types. There is much in favour of Almquist's views and I think his method must result at least in bringing together similar-looking plants. *R. lutetiana* and *R. dumetorum*, for example, find a place side by side in the Caninæ section under species-type *cuneatula*, the former a *vir.* form, the latter a *virf.*

The need for some such system in dealing with our British Roses is obvious, but an entirely new classification should not be attempted until the support of experimental evidence is forthcoming. Cultural results will not be obtained without the expenditure of much time and patience, but even if a single aggregate species like *R. canina* L. were submitted to systematic crossing and fully worked out along the lines of Mendelian research, we should obtain results, I think, which would form a real contribution to our knowledge of this most difficult genus.

I do not wish, at present, to enter very far into the controversy as to how many names should be retained or how many more should be invented. If it be proved that elementary species arise and remain stable it may be desirable to name such forms as the natural units of classification, but in the present state of our knowledge, the creation of innumerable names in a genus like Rosa, seems to be devoid of all scientific principle and is much to be deprecated. I would at present strongly support any systematist who returned to the Linnean conception of the species, denoting its various combinations by some purely symbolical method.

In conclusion I wish to mention that the present contribution has grown out of a correspondence with Mr. A. G. Tansley, F.R.S., on some of the questions that have here been discussed, and I gladly take this opportunity of expressing my thanks to him for the great interest he has shown in its preparation.

POSTSCRIPT.

Since the above paper was written Colonel Wolley-Dod has made a further contribution to the study of the genus under the title "A Revised Arrangement of British Roses," published in the *Journal of Botany*, 1920. The author has reached the conclusion that "most of the very detailed descriptions of Déséglise, Ripart and others can hardly be other than those of an individual bush or specimen, which cannot be completely matched by any other," and in consequence of his conviction of the worthlessness of nearly all the so-called species of these authors, he has reduced the number of names having full specific rank to eighteen. We find, for example, in the large subsection Eu-caninæ only five species—*R. lutetiana*, *R. Blondæana*, *R. dumetorum*, *R. Reuteri* and *R. tomentella.* It is true the author still retains a formidable list of names under most of the species, but these are never accorded more than varietal rank and many are regarded simply as forms.

REFERENCES.

Almquist, 1918. *Rosa* in Lindman's *Svensk Fanerogamflora*, Stockholm.

Baker, 1869. Monograph of British Roses. *Journ. Linn. Soc. Bot.* XI.

Barclay, 1899. Further Notes on Scottish Roses. *Ann. Scot. Nat. Hist.*

„ 1910. Perthshire Roses. *Proc. Perths. Soc. Nat. Sci.* V., Pt. II.

„ 1915. Notes on Roses, Part I. *l.c.* VI., Pt. II.

„ 1916. Notes on Roses, Part II., *l.c.* VI., Pt. III.

Bateson, 1913. Mendel's Principles of Heredity.

Brainerd, 1906. Hybridisation in the Genus Viola. *Rhodora*, VIII.

„ 1907. The Behaviour of the Seedlings of certain Violet Hybrids. *Science.* N.S. XXV.

Cole, 1917. Imperfection of Pollen and Mutability in the Genus Rosa. *Bot. Gaz.*, LXIII.

Crépin, 1869. Primitiæ Monographiæ Rosarum. *Bull. Soc. Roy. Bot. Belg.*, VIII.

„ 1892. Tableau Analytique des Roses Europėenes, *l.c.* XXXI.

Christ, 1875. What is *Rosa hibernica* of Smith ? *Journ. Bot.* IV.

„ 1884. Allgemeine Ergebnisse a.d. systematischen Arbeit am Genus Rosa. *Botan. Centralb.*, V., 18.

Jeffrey, 1914. Spore conditions in hybrids and mutation hypothesis of De Vries. *Bot. Gaz.*, LVIII.

Matthews, 1910. On some British Hybrid Roses. *Trans. Bot. Soc. Edin.*, XXIV., Pt. III.

Moss, 1912. The Intern. Phytog. Excur. in the British Isles. XII. Remarks on the characters and nomenclature of some critical plants. *New Phytol.* XI.

Parmentier, 1898. Recherches Anatomiques et Taxinomiques sur les Rosiers. *Ann. Sci. Nat.*, VI.

Traaen, 1911. Scandinavian Roses. *Journ. Bot.*, XLIV.

„ 1913. Rosa Afzeliana. *l.c.* LI.

Trow, 1912. On the inheritance of certain characters in the common groundsel—*Senecio vulgaris*, Linn.—and its segregates. *Journ. Genetics*, II.

Wolley-Dod, 1908. The Subsection Eu-caninæ of the genus Rosa. *Journ. Bot.*, XLVI.

„ 1910. The British Roses (excluding Eu-caninæ), *l.c.* XLVIII.

„ 1911. A List of British Roses, *l.c.* XLIX.

„ 1920. A revised arrangement of British Roses. *Journ. Bot.*

MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER VI.

Presumptive Mutations in Wild and Cultivated Plants.

OBVIOUSLY, if the mutation theory is to be of any use the conceptions derived from controlled breeding experiments must be applicable to plant and animal species and varieties as they occur in nature. A beginning has only been made in this vast field of application, but it is sufficient to show that the mutationist conception of germinal changes is widely applicable to the variations observed among wild species. As an aid in the analysis of the populations that go to make up a wild species it is undoubtedly of great service, and its illuminating influence is also beginning to make itself felt in the fields of systematics, phylogeny and relationships. Innumerable records of species, varieties and forms in the literature of systematic botany and zoology and the journals of naturalists show how universal is the incidence of this principle.

That the relationships and origin of nearly related species can also in many cases be most clearly interpreted in terms of unit differences has been shown by Bateson (1913) for the North American warblers (Helminthophila) and flickers (Colaptes) and other forms. In plants, the same principle has been applied (Gates, 1916) to species of Spiranthes, Clintonia, Streptopus, Maianthemum, Ranunculus, Actæa and Spiræa, and in a preliminary way to the genus Trillium (Gates, 1917b). Similar analytical conceptions have been applied to the differentiation of species and varieties, their relationships and phylogeny, in the North American Melanthaceæ (Gates, 1918a) and Convallariaceæ (Gates, 1918b). The results are in no sense revolutionary, but wherever the mutational principles are applicable they do appear to give a more clear-cut and accurate analysis of specific differences, and also of the phylogenetic and distributional relationships within a group. Moreover, there is the beginning of a physiological element in classification on these principles, which is a distinct gain. More recently Small (1917-19) has successfully applied these principles to a study of the development of the Compositæ.

It is obvious that in older groups, and wherever extinction has taken place, the actual succession of mutations in the development of any group will be obscured or lost altogether. These principles can be most readily and widely applied to modern expanding groups

in which the origin of new divergent characters is now or has recently been taking place.

Turning now to the recorded cases of mutation in the literature, they form such an array that it would be a colossal task to attempt even to enumerate them. The condition is so common in flowering plants that it may be considered exceptional to find a species without any mutational varieties. A few instances will be selected, almost at random, for mention here. First we will consider doubling.

Doubling.

The gardeners' tradition that "doubling" or the transformation of stamens into petals,[1] is a result of cultivation has long been disproved. It is evident from the records that doubling of flowers occurs "spontaneously" both in wild and cultivated species. It is a typical mutation, although the completeness of the transformation of stamens into petals, and the associated changes in the flower, may vary in different cases. Breeding experiments have shown that the double condition is in some forms a Mendelian dominant, but more usually a recessive. Bateson (1909, Chap. XI) has considered the cases studied before 1909. The work of Miss Saunders on the inheritance of doubleness has been most ample, and some of her results may be summarized here. Taking the simpler cases first, she finds (1917) that in the Welsh poppy, *Meconopsis cambrica*, doubleness is dominant, the F_2 from a cross containing three doubles to one single. The doubleness results from a variable degree of petalody of the andrœcium and gynœcium. In the hollyhock (*Althæa rosea* and *A. ficifolia*) the F_1 is intermediate and the F_2 gives the 1 : 2 : 1 ratio, *i.e.*, neither condition dominant; in carnations (*Dianthus caryophyllus*) doubleness is a simple dominant,[2] while in sweet william (*D. barbatus*) singleness is dominant and the F_2 from a cross contains three singles to one double.

In *Chelidonium majus* Sax (1918) finds that doubleness is apparently a simple recessive, but the F_2 gives a continuous series from singles to full doubles. Statistically considered, there is much

[1] Doubling may also occur, as in Fuchsia, by an increase in the number of petals without any change in the stamens, or it may result from change of carpels to petals, or from all these conditions combined.

[2] According to the breeding work of Norton and of Batchelor the doubleness of carnations appears to be of two distinct types or degrees, full doubles and standard doubles, the latter having some stamens. Full double × single gives an F_1 which is standard double, and an F_2 with the three types in the ratio 1 : 2 : 1. Miss Saunders finds, however, all degrees of doubling in the DD's and DR's, which are therefore indistinguishable.

greater variation in the doubles than in the singles, and a high negative correlation between petal number and stamen number in F_2 plants, as would be expected if stamens are replaced by petals.

The more complicated cases of doubling have been elucidated by the well-known work of Miss Saunders on Petunia (1910, 1916a, 1916b), Matthiola (1911, 1913, 1915a, 1915b), and the wall flower *Cheiranthus cheiri* (1916c, 1917). According to Frost (1915), doubleness is dominant in Petunia, and Miss Saunders (1916b) concurs in this statement to the extent of finding that all true-breeding singles of *P. violacea*, *P. nyctaginiflora* and various garden strains, when pollinated from doubles give an F_1 containing both singles and doubles. This indicates the heterozygous character of the doubles, and hence the dominance of doubleness over singleness. But since the doubles are sterile and *P. violacea* itself is a self-sterile species it has not yet been possible to eliminate the possibility that singleness is dominant, though Frost's hypothesis of selective sterility accompanied by dominance of doubleness would appear to fit the facts. In the wallflower, as in sweet william, singleness is dominant.

In the case of Stocks (Matthiola) the prolonged experiments of Miss Saunders have gone far to clear up the hereditary relationships. Singleness is dominant, and it is well-known that in the various strains both pure-breeding and double-throwing (eversporting) singles occur. The inheritance of singleness or doubleness is independent of the pair of Mendelian characters for hoariness or smoothness, and also of cell-sap colour, but is linked with plastid colour (whether white or cream). All the singles derived from an eversporting individual appear again to throw doubles. And in all cases there is an excess of doubles in the offspring in the ratio of something more than 7 singles : 9 doubles, from which it is concluded that two factors are primarily concerned in producing a single or a double.

Moreover, breeding experiments show that all the functional pollen grains of eversporting individuals carry doubleness, while some of the ovules carry the factor for doubleness, and some that for singleness, in the above proportion. Miss Saunders (1911) explained the absence of doubles in the offspring of true-breeding singles when crossed together, by an unequal distribution of the factors among pollen grains and ovules. In the light of more recent work it is probably simpler to explain the fact that some singles breed true by assuming linkage of one determiner to a lethal

factor. This does not of course explain the important fact of differential viability of certain types of gametes as between pollen and ovules.

Miss Saunders assumes that singleness in stocks is due to the presence of two factors X and Y, that in the eversporting singles these two factors show partial coupling, and that they are both carried only by the ovules. Also a factor W represents colourless plastids, while in cream forms that breed true W is absent. There is also a sulphur-white race, heterozygous for W, in which W is present in some of the ovules but absent from the functional pollen. This relationship appears to be explained by coupling of W with either X or Y. Again, in the singles which breed true for singleness it is assumed that X and Y are linked, so that in crosses with eversporting singles recombinations cannot occur. These complicated relationships of factors are quite in harmony with results obtained from breeding experiments with other organisms.

Another feature of the double stocks is that they show greater viability than the singles, and hence appear in a higher percentage from old seed and also when the more vigorous plants are selected before flowering.

The various varieties of stocks must have originated through mutations, and Miss Saunders (1915b) traces the historical order of their appearance.

In Fuchs' herbal (1542) the purple, red and white forms were already known, but Ruellius a few years earlier makes no mention of the red. The purple and white varieties of *Matthiola incana* date back to Dioscorides. The first record of the double stock appears to be in Dodoens' herbal (1568). This is also the first European record of the double wallflower. Double violets are apparently first mentioned in a work published in 1535.

The records indicate that the double stock perhaps originated in cultivation in some Dutch garden, and they show that it was completely double and sterile from its first appearance—no doubt a mutation. Sowerby (*Eng. Bot.*)[1] figures a hoary stock obtained from the cliffs of Sussex in 1806. This shows partial doubling in some flowers. The species must have independently developed a factor for doubling in this locality.

Frost (1912) describes an "early" dwarf mutation with few nodes from ten-weeks stocks. It is said to behave as a simple Mendelian dominant, but the evidence is not very clear.

[1] See Saunders (1917).

A much earlier record of a double wallflower has, however, since been found (Saunders, 1916c). There is a reference to it in an Arabic "Book of Agriculture" of the 12th Century, the statements in which are based on an earlier work probably written about 1073. As we shall see, the records show that doubling is by no means rare in wild species, so it is quite possible that a double wallflower was taken into cultivation as such. Doubling appears to have occurred at least twice in cultivation. The older, fully double wallflower (Saunders, 1917) was wholly sterile like the double stocks. It appears to have originated only once as a sport, and have since been propagated by cuttings. The partial double is more recent in origin and shows grades of doubling forming a continuous series. This double form is therefore not in the same series with the full double, but represents an independent germinal change.

Bateson and Miss Sutton (1919) have found greater irregularity in Begonia. A double monœcious ♀ × single ♂ gave singles generally dominant, but segregation was irregular and transitional forms appeared. An average of 1 double in 32 was obtained, and back crosses were also irregular. *B. Davisii* from Peru crossed on common doubles gave only double. This single is believed to be genetically double on the ♂ side.

The first double Dahlia is mentioned and figured in a work on the natural history of Mexico, published at Rome in 1651.[1] Hence it apparently did not originate in cultivation. There are a number of early American records of wild species with double flowers, some of which may be summarized here. In *Saxifraga Virginiensis* we have found nine records of double flowers, as follows: (1) A double found near Hingham, Mass., in 1849.[2] (2) Asa Gray[3] found a double at Dawers, Mass., 1866, which continued so from year to year. (3) A specimen found on the Delaware River below Easton with extra petals.[4] This was apparently not fully double. (4) A wild double from Canaan, Conn., was reported by A. Gray.[5] It bore 70 or 80 flowers, all pure white and fully double, without stamens. This very ornamental plant was divided, and part of it cultivated in the Cambridge, Mass., Botanic Garden. (5) Two more specimens were found[6] on the banks of the Schuylkill, near

[1] Gard. Chron. 59: 336, 1916.

[2] J. L. R., Amer. Nat. 2: 610, 1869.

[3] Amer. Nat. 2: 484, 1869.

[4] Porter, Thos. C., Bot. Gazette 1: 5, 1875.

[5] Amer. Nat. 11: 366, 1877.

[6] Martindale, I. C., Amer. Nat. 11: 432, 1877.

Philadelphia, having larger flowers than in the previous case. (6) Meehan[1] records finding a double on the Wissanickon about 1854. (7) One near Beverly Bridge, Mass.,[2] with panicle smaller than normal, the flowers full double, petals replacing both stamens and pistil. (8) Meehan[3] reported a double from North Woburn, Mass. These records, through trivial enough in themselves, acquire interest when considered as a whole. For they show that in a large part of its area and for over a quarter of a century *S. Virginiensis* was producing sporadic doubles as mutations. It is probably doing so still, and it may be that, as in stocks, some individuals are eversporting, giving rise to fresh doubles in each generation.

Before leaving Saxifraga we may point out some of the other derivative forms which have been described in this genus. Sterns[4] describes a form of *S. Virginiensis* on Manhattan Island which he called var. *pentadecandra.* In two plants observed nearly all the flowers had 15 stamens, the extra 5 replacing the petals. In these apetalous flowers the stamens were exposed in the bud. Such a change of petals to stamens is relatively rare. Several other plants in this location had apetalous flowers, but the stamens were ill-formed and more or less aborted. Three more specimens were found[5] in the locality in the following year. The same variation occurs in the cultivated European species *S. granulata,* as recorded by Masters.

This must be regarded as a case of parallel mutations. In *S. crassifolia* an abnormal increase in the number of pistils has been repeatedly observed, while *S. Virginiensis* var. *chlorantha* Oakes was described from Topsfield, Mass., 1847, having tiny green pubescent petals.[6] Var. *pentadecandra* was found in profusion in a slate rock locality in Essex Co., Mass. The Saxifrages are evidently subject in the wild condition to many mutations besides doubling.

Thalictrum anemonoides is another species for which there are a number of records of doubling. A semi-double found near Cincinnati, Ohio, in 1834 was taken into cultivation and in five years

[1] Amer. Nat. 2: 484, 1869.

[2] Russell, J. L., Am. Nat. 3: 327, 1869.

Amer. Nat. 6: 487, 1872.

[4] Sterns, E. E. Some anomalous forms of *Saxifraga Virginiensis.* Bull. Torrey Bot. Club 14 : 122—125, 1887.

[5] Bull. Torrey Bot. Club 15: 166, 1888.

[6] See also Rhodora 19: 143, 1917.

produced full double flowers.[1] Many other instances of doubling in this species are on record from Asa Gray, Thomas Meehan and others. Doubles are also recorded in many species of Ranunculus. Thus *R. rhomboideus* is sometimes found double in Floyd Co., Iowa.[2] One such specimen was transplanted and continued to produce only double flowers. A specimen of *R. repens* L. collected near Camden, New Jersey, had 10 petals (an extra whorl).[3] *R. multifidus* Pursh at Grand Rapids, Mich., frequently has double and quilled flowers, often with the scales (nectaries) changed to tubular appendages.[4] *R. acer*, *R. bulbosus* and *R. ficaria* are all said by Meehan[5] to have double forms. He points out that doubling is rarely due to cultivation, although numerous double forms of Ranunculus now occur in seed catalogues.

Records of doubling in the Canadian mayflower, *Epigæa repens*, also abound, though the change is not so regular as in other forms, there being great variation in the nature of the doubling. A specimen from Worcester, Mass., continued to produce doubles for several years.[6] The stamens were partly converted into petals, the outer series being more or less coalescent into a tube. Other records are from New Brunswick and Massachusetts, the latter being a specimen with flower having three corollas, one within the other, the stamens absent or abortive.[7] At Plymouth, New Hampshire, double flowers were observed[8] year after year, with great variation in the degree of doubling. Three-fourths had two whorls of 5 petals each, and 5 stamens alternate with the inner petals. In a few flowers nearly all the 10 stamens were transformed into petals, and in all the carpels were transformed to leaves.

In *Hepatica triloba* Gil. one specimen with strongly double flowers was found (Hilbert, 1913) near Sensburg, Germany, in 1894, surrounded by singles. In 1912 another double specimen with blue flowers was found in the same place. It was transplanted to a garden and flowered double the following year, but gave no seeds. The stamens were changed to petals. There is also in cultivation

[1] Amer. Nat. 2: 610, 1869.

[2] Arthur, J. C., Amer. Nat. 6: 427, 1872.

[3] Bot. Gazette 1: 5, 1875.

[4] Bot. Gazette 2: 90, 1877.

[5] Amer. Nat. 2: 484, 1869.

[6] A. Gray, Am. Nat. 6: 429, 1872.

[7] Bailey, W. W., Bot. Gaz., 6: 238, 1881.

[8] Wilson, Kate E., Bot. Gaz. 15: 19, 1890.

a strongly double red form. A double *Anemone Pulsatilla* is figured by Helwing as early as 1719. Doubling is well-known to be of frequent occurrence in the Ranunculaceæ. A *Convolvulus sepium* with double flowers is described from New Brunswick, New Jersey.[1]

An interesting record is that of *Sagittaria variabilis*,[2] Engelm., a large patch of which, on an island in the Susquehanna, had completely double flowers. All the carpels of pistillate flowers and all the stamens of staminate flowers were converted into petals, giving the flowers the appearance of tiny snowballs. This probably represented a single individual mutation which had spread from rootstocks Elsewhere (Gates, 1917b) we have assembled numerous records of doubling in *Trillium grandiflorum*, the same root stock producing each year a double flower. There are various interesting records of double wild Rhododendrons. Rehder (1907) found in the woods at Glacier, British Columbia, a bush of *R. albiflorum* Hook. with double flowers. It was growing among normal bushes. In the double flowers, petalody of the stamens was combined with an increase in the number of staminal whorls. In the Alps, *R. ferrugineum* has been observed at least twice with double flowers, Kerner having found a large number of such shrubs in one locality. Miyoshi (1910) has described the occurrence of doubles in *R. brachycarpum* Don. The double form is called var. *Nemotoi* Makino. In the location (on a volcanic mountain) where it was found both white and rose varieties occur, but only the white showed doubling. Seven plants were observed with double flowers and ten with normal. In another place a group of five bushes was found, all with double white flowers. Nakai[3] found double and white varieties of *R. Kaempferi* in the vicinity of Karume, Japan.

That cultivation does not produce doubling, even in a genus where doubles occur wild as mutations, is clear from the case of *R. Metternichii*, which is much cultivated in Japan but no double is known. If there is any relation between the environment and the occurrence of mutations in this genus, it remains elusive, as in most other organisms. We still have no better term than "spontaneous" to apply to it.

Makino[4] cites also the finding of one double *Oxalis corniculata*, and *Deutzia scabra* entirely double in a locality in Nikko.

[1] Bull. Torrey Bot. Club, 17 : 238, 1890.

[2] Porter, Thos. C., Bot. Gazette 1 ; 5, 1875.

[3] Bot. Mag. Tokyo, 29 : 261, 1915.

[4] Journ. Coll. Sci. Tokyo, 1910.

In a study of the variations of tobacco in the East Indies, Lodewijks (1911) states that double flowers are the most common aberrations, although gigantism, fasciation and other types of change also occur. Doubles appear yearly on almost every plantation, and the doubling is of the hose-in-hose type. All parts of the plant are also changed, so that doubles can easily be distinguished before they come into bloom. The stem is zig-zag, shorter and not winged; the leaves are very small and thicker owing to local outgrowths on their ventral surface; the midrib is twisted, and the stigma shows similar growths, though to a less extent. All these peculiarities apparently result from a single mutation, and the type breeds true. In crosses with the normal the latter dominates almost without exception, and the F_2 gives a 3 : 1 ratio (46S : 10D, 306S : 105D). It is a curious fact that the heterozygotes were distinguishable from pure singles by their leaves having outgrowths on the underside. Thus of the 306 singles above, 204 were shown in this way to be heterozygous and 102 SS. Again, in the F_2 from single × double the ratio was 32S : 58DS : 31D. It is very interesting that in this set of mutant characters, the double flowers are wholly recessive and the leaf peculiarity at least partially dominant, though they behave as a unit in inheritance.

In a work on the mountain cherries of Japan, in which is embodied an elaborate study of the group of plants which plays such a prominent part in the national life of that country, Miyoshi (1916) recognizes four species, *Prunus serrulata* Lindl., *P. mutabilis* Miyos., *P. sachalinensis* (Fr. Schm.) Miyos., and *P. fruticosa* Miyos., and a very large number of forms, especially of *mutabilis* (65) and *serrulata* (68). Cultivated double varieties have been known for over a thousand years. A great number of forms have arisen in the intervening period, but only the best have been preserved and many old varieties have been lost. In Yoshino, the oldest and most famous cherry neighbourhood, trees have from time to time been planted from the neighbouring mountains for over a thousand years. At Koganei, near Tokyo, is the greatest assemblage of wild cherries, none of which show any influence of cultivation. There are three other main centres for cherry varieties, and many places noted for a local form or even a single tree, but the larger centres have been the source of new forms and races from time immemorial.

From a study of the early records, Miyoshi concludes that a large number of cultivated sorts existed two centuries ago, and has been largely added to during the last hundred years. The many forms which receive botanical names for the first time are distinguished by such features as leaf colour, flower colour, singles or doubles, fragrance, inflorescence, and pubescence. The multiformity of the group is comparable with that of the North American Cratægus, or with *Draba verna* or *Viola tricolor*, and the forms appear to have arisen as mutations. Seeds in most cases yielded a uniform offspring, but it seems possible that some mutational characters may have been transferred by crossing.

Peloria.

Peloria, or the sudden development of actinomorphic flowers in a zygomorphic species, has been studied most extensively in the Scrophulariaceæ where it occurs most commonly, although it is also found in the Labiatae, Leguminosae, Orchidaceæ and other families with zygomorphic flowers. It is of evolutionary interest because zygomorphy is supposed to have been gradually developed in relation to the visits of insects, while peloria is a sudden re-expression of symmetry.

Peloria behaves in part as a recessive character, is known to occur as a variation in numerous wild species, and in a few cases has become a specific character, indicating that in such cases zygomorphy is not essential for survival. De Vries[1] studied peloria in *Linaria vulgaris* for thirteen years and gives the literature of the subject up to the time of his work. He mentions *Mentha aquatica* as a species whose apical flowers are always peloric, and *Uropedium Lindenii*, found in Colombia, as the peloric form of *Cypripedium caudatum*. It is not impossible that the Ranunculaceous genus Aquilegia, with its five spurs, arose as a peloric mutation from a zygomorphic one-spurred ancestor. The increased number of nectaries should give it an advantage as regards insect visits.

The genetical studies of peloria appear to have been confined to the Scrophulariaceæ, but in this family the genera Linaria, Antirrhinum and Digitalis have given valuable results. The earliest discovery of a peloric condition in *Linaria vulgaris* was made by Zioberg in 1742. On an island near Upsala he found among the normal a plant bearing only regular flowers, and Linnæus described it under the name *Peloria*. There are numerous later records of

[1] The Mutation Theory, Vol. II.

the same wild mutation elsewhere. The flowers have five spurs and this type is now known as *peloria nectaria*. There is another type, *peloria anectaria*, in which the flowers are actinomorphic, but without spurs. Another race studied by de Vries, which he called *hemipeloria*, produces usually a single (terminal) peloric flower on each plant. Such a flower may not appear in some years, or occasionally more than one may appear, and this seems to be controlled to some extent by the environment, but the capacity for producing a peloric flower is evidently inherited through the seed. In breeding from such a half-race de Vries finally obtained mutations to the full peloric condition, in the fifth and sixth generations of culture. This mutation occurred with a frequency of about 1%, and although highly sterile it probably breeds true. Whether there are any plants which never produce a peloric flower is uncertain.

A similar peloric condition (*Digitalis purpurea monstrosa*) has long been known in foxgloves, in which a single, erect terminal peloric flower occurs on the plant, and opens before the other flowers, which then follow in acropetal succession. The peloric flower frequently also shows an increase in the number of parts. This condition is found by Keeble, Pellew and Jones (1910) to be inherited as a simple Mendelian recessive. The peloric flowers are perfectly fertile with their own pollen, the inheritance being the same through peloric or normal flowers of the plant.

In *Antirrhinum majus*, as in many other plants with zygomorphic flowers, sporadic peloric flowers occasionally occur. There is also a completely peloric race, which Baur (1911) used in his extensive crosses. He concluded that zygomorphy depended upon the presence of two factors P and E. In the absence of E the plant will have only peloric flowers, but plants having E without P (EEpp) produce *both* peloric and normal flowers. This is an interesting case of somatic segregation in the presence of one pair of factors, and presumably there would be no difference in inheritance from the two types of flower on the same plant. If such an EEpp individual is crossed with a fully peloric race (eePP), the F_1 (EePp) bears only normal flowers, while the F_2 gives (1) normal-flowered plants, (2) plants with both normal and peloric flowers, (3) plants with only peloric flowers, in the ratio 9 : 3 : 4. The numbers actually obtained were 70 : 13 : 45, and the departure from expectation (72 : 24 : 32) is explained by the fact that badly nourished plants belonging in class (2) produce only peloric flowers

and hence fall in class (3). Bateson (1902) first pointed out that in reciprocal crosses made by Darwin between normal and peloric snapdragons, the peloric character behaved as a simple Mendelian recessive, giving 90 non-peloric to 37 peloric in F_2. Darwin, however, speaks of two of the 90 plants as being "in an intermediate condition between the peloric and normal state." The exact nature of these intermediate plants is not clear. If they correspond to Baur's class (2), then the actual numbers 88 : 2 : 37 should be compared with an expectation of 72 : 24 : 32 for the ratio 9 : 3 : 4. Hence if the behaviour was the same as Baur describes there would be a large excess of normals to account for, and a corresponding defect of "intermediates."

It is thus obvious that peloria, like doubling, though originating through mutations, behaves differently in different genera.

Other mutations in wild and cultivated plants.

These records are sufficient to show the frequent occurrence of doubles in wild species as parallel mutations, and also of peloria, especially in the Scrophulariaceæ. That they are obviously not in any phylogenetic line of descent however, and are more or less incapable of reproducing themselves, detracts somewhat from their evolutionary interest. We may therefore consider some other types of polymorphism which have arisen in wild species or in cultivation. It has been found practically impossible to draw a line between mutations occurring in controlled cultures and the obviously similar changes which are frequently found wild. We therefore feel justified in extending the mutation conception to these wild forms and varieties.

Linaria alpina, a species of the Alps and Pyrenees, has two varieties, *rosea* and *concolor*, whose genetic relationships have been investigated by Miss Saunders (1912). In the typical *alpina*, which is most common in the Alps, the corolla is blue, with an orange palate, which is partly due to the presence of a viscous orange-yellow fluid in the epidermal cells and the hairs of the beard and partly to the yellowish colour of the cuticle. The var. *rosea*, which is rare and confined to certain stations, is pink with orange palate and behaves as a simple recessive to the type. Var. *concolor* is blue without the orange palate, and this is dominant to the type. Each of the varieties therefore differs from the type by one factor, but it is uncertain which was the original form. In *L. vulgaris*, which is yellow with orange palate, de Vries[1] found on crossing with

[1] Mutationstheorie, II, p. 152.

var. *perlutescens*, which is yellow throughout, that the yellow palate was dominant. Thus yellow palate is dominant in one species and recessive in the other—a quite unexpected result. It is evident that dominance or recessiveness cannot safely be used in determining which is the original or parental type. Even though these are parallel mutations, the alternation in dominance probably depends on an effect of the other specific differences.

In *Digitalis purpurea* several varieties, evidently mutations, have been studied. Saunders (1911), Shull (1912) and others have bred the form called by Chamisso *heptandra* in 1826. The flowers are characterized by dialysis and staminody of the corolla, giving a flower with a petaloid upper lip and seven stamens. But many flowers of a heptandrous plant may show the abnormality in varying degrees, like a wave of reversion advancing up the plant. This variety is a recessive in inheritance.[1] A form *nudicaulis* with smooth stems and leaves less hairy on the upper surface is found by Miss Saunders (1918) to be a simple dominant to the type. Although this condition corresponds to the half-hoary type in stocks, yet in the latter it is due to several factors and behaves as a Mendelian recessive to hoary. This is another example of externally similar characters which are wholly different in their genetic relationships, and it shows that certainty regarding variety relationships can only be attained by actual breeding experiments. *D. purpurea nudicaulis* occurs wild in various parts of England mingled with *pubescens*, the hairy type. The latter is usually more abundant and the indications are that *nudicaulis* has originated from it as a mutation. That a new dominant character can arise by a mutation is known from the case of *Œnothera rubricalyx* among plants or such mutations as bar eye in Drosophila among animals.

From an almost unlimited number of cases of new varieties or forms probably originating as mutations in wild species and often already in process of spreading, we may select a few almost at random.

[1] An exactly parallel mutation has long been known in a North American member of the Ericaceæ, *Kalmia latifolia*. In 1871 Asa Gray (Am. Nat. 4 : 373) described a plant from South Deerfield, Mass. showing dialysis with staminody. It was grown in the Arnold Arboretum and figured by C. S. Sargent (Garden and Forest 2 : 452). It seeds freely, but apparently its inheritance has not been tested. In 1909 Stone (Rhodora 11 : 199) independently reported the same form (var. *polypetala* Nicholson) from the roadside in Leverett near Mt. Toby, and Rehder (Rhodora 12 : 1, 1910) adds a number of varieties, evidently mutational, of this species. Fernald (Rhodora 15 : 151, 1913) records near St. John's, Nfld., a considerable colony of *K. angustifolia* with white corollas (forma *candida*). This form was also found at Sherborn, Mass., and evidently occurs as a sporadic negative mutation which will spread if left to itself.

The ordinary poison ivy, *Rhus toxicodendron* of North America, has fruits glabrous or nearly so. A. H. Moore,[1] records from Bristol, Maine, a form *malacotrichocarpum* with fruits abundantly pilose. *Oxalis stricta*, var. *viridiflora* was described by Hus from St. Louis,[2] differing from the type in having green petals. The same form was afterwards found in plenty by Bartlett[3] near Thomson, Georgia, doubtless arising from an independent mutation. The petals are broader, apparently owing to a change in the shape of the cells, and the presence of chloroplasts may perhaps represent an independent change. *Melica* (*Avena*) *stricta* Michx. has glumes strongly tinged with purple. Forma *albicans* Fernald,[4] the prevailing form on some of the mountains of Maine and Eastern Quebec, has glumes whitish or pale straw-coloured. *Drosera rotundifolia* var. *comosa* is a dwarf variety found by Fernald[5] in a bog at the mouth of the Grand River, Gaspé Co., Quebec. It has a sub-capitate inflorescence of few flowers, petals coloured, and the ovary tending to develop into a rosette of grandular leaves. This dwarf occupied a considerable area in abundance almost to the exclusion of the normal. It is evidently a mutational form able to survive in favourable conditions.

Gaylussacia resinosa, the common huckleberry of America, has black berries without a bloom. Var. *glaucocarpa* Robinson is common in Eastern Connecticut[6] where it occurs in distinct clumps generally associated with the species, from which it differs in having blue glaucous fruits and also in its greater vigor and glaucous leaves. Fernald (1917) describes a colony of *Bidens* by Lake Pocotopaug, Connecticut, which differs from the species *B. connata* of that region in having flat 2-awned achenes like *B. heterodoxa* of Prince Edward Island. He interpretes it as an outlying colony of the northern species, but since its leaves resemble *B. connata* and its var. *petiolata* it more probably represents a parallel mutation.

The American saxifrage, *Tiarella cordifolia* L., extends from New England to Minnesota and southwards. In Maine, New Hampshire and Vermont two forms are found.[7] The plants differ

[1] Rhodora, 11 : 162. 1909.

[2] Rept. Mo. Bot. Garden, 18 : 99, 1907.

[3] Rhodora, 11 : 118, 1909.

[4] Rhodora, 7 : 244, 1905.

[5] Rhodora, 7 : 8, 1905.

[6] Sheldon, J. L., Rhodora, 4 ; 14, 1902.

[7] Danforth, C. H., 1911. A dimorphism in *Tiarella cordifolia*. Rhodora, 13 : 192-3.

in a single character, having yellow or orange anthers. This is due to a difference in the pollen, which is clear yellowish green in one form and reddish brown in the other. The latter colour is caused by the presence of an orange colouring matter in the cytoplasm, which exudes through the cell wall when the pollen is placed in alcohol or water. Both types of pollen germinate, and plants with the yellow type of pollen appear to be at least twice as numerous as those with the orange pigment. This is of particular interest as showing dimorphism in a gametophytic character.

Leptospermum scoparium is a polymorphic shrubby species occupying vast tracts of New Zealand, with a series of forms also in Tasmania and Australia. It has conspicuous white flowers sometimes stained with pink. In the north of North Island (Cockayne, 1907) a variety is abundant having invariably pale pink flowers, the colour in the petals being confined to the base of the claw. About 1897 a plant was discovered in Otago having petals bright rose colour over their whole surface. This form is known in commerce as *L. Chapmani* and is multiplied by cuttings. Later, on the sandhills 200 miles from where *Chapmani* originated, a plant with rich crimson flowers, was found. It also differed in its more slender, drooping habit, darker foliage, and the flowers were not terminal. From open-pollination a few seedlings like the type were obtained. The evidence indicates that the polymorphism of this species is due to mutation, two of the forms having already established themselves as local varieties.

Coreopsis tinctoria Nutt. is an annual North American Composite, often cultivated and escaped from gardens. It is polymorphic, producing (1) dwarfs, and forms with (2) brown ray florets, (3) tubular ray florets and (4) ligulate disc florets. Raciborski (1908) found in an escaped colony near Lemberg a peculiar type first described by Al. Braun in 1870. It has numerous adventive shoots arising on the internodes and also on the under surface of the leaves along the midrib and was called var. *prolifica*. The seeds from such a plant with brown rays yielded 84 offspring, all but 11 of which showed the adventive shoots. Some of the latter were tall, some short, and a few had yellow rays. Seeds of another (yellow) *prolifica* gave 420, of which all but 16 showed the abnormality. This indicates that the abnormality is probably a recessive, the normals being due to vicinism. Normal plants, however, never gave seedlings with the abnormality, nor could it be produced by wounding or cultivation on rich soil.

Fernald[1] describes *Silene antirrhina*, L. forma *Deaneana* as differing from the type only in the absence of the glutinous band found on some of the internodes in the type. This form is occasional throughout the range of the species, and is constant in the colonies where it occurs. A considerable number of mutations in wild species are given by Hus (1911), and a number of others have been discussed by the writer[2] in their relation to phylogeny. *Betula nana*, L. var. *Michauxii*, of Newfoundland and adjacent portions of Canada,[3] differs from the type chiefly in that the bracts of the pistillate aments are commonly simple and oblong instead of 3-lobed. Similarly *B. alba*, L. var. *elobata*, Fernald, which occurs on Mt. Albert in Gaspé Co., Quebec, differs from the type in the same respect and is evidently a parallel mutation. Near New Boston, New Hampshire, a tree of *B. lenta* was found having deeply serrate leaves,[4] a unit variation. Laciniation of leaves and petals is one of the commonly recorded types of variations in plants.

Rhamnus caroliniana, Walt. is glabrous or glabrate. The var. *mollis*, Fernald[5] differs in having its leaves densely velvety beneath. The pubescent variety occurs in different parts of the range of the species. There is no evidence as to which is the older type. In *Erigeron ramosus* the reverse change has apparently taken place. Var. *septentrionalis*, Fern. and Wieg.[6] differs in having greener foliage, the leaves being sparsely hispidulous or nearly glabrous, instead of cinereous-strigose. The glabrous variety is more northern than the species, occurring in Newfoundland, Eastern Canada, New England and Idaho. This may be because it is better adapted to a cold climate, or merely because it happened to arise in a more northern latitude, but the former seems more probable. A number of species have northern glabrous varieties, but in other species a pubescent variety of a glabrous species is more northern in its distribution. A somewhat different case is found in *Fragaria Virginiana*, var. *terræ-novæ*,[7] which differs from the type in having the pubescence of the petioles and leaves closely appressed. The variety is abundant in Newfoundland, Southern Labrador, and the Gaspé Peninsula where the type is a rarity. It occurs as far

[1] Rhodora, 17 : 96, 1915. Also 12 : 129, 1910.

[2] Gates (1917c).

[3] Fernald, M. L., Rhodora, 15 : 168, 1913.

[4] Sanford, S. N. F., Rhodora, 4, 83, 1902.

[5] Rhodora, 12 : 79, 1910.

[6] Rhodora, 15 : 59, 1913.

[7] Fernald and Wiegand. Rhodora, 13 : 106, 1911.

south as Maine and Vermont, where type and variety sometimes occur together in the same colonies.

The sunflowers of the middle Western States of America are a polymorphic group represented by great numbers of individuals. In 1910 a single mutant of *Helianthus lenticularis* with red instead of yellow rays was found at Boulder, Colorado by Cockerell (1912). It proved to be heterozygous and has since behaved as a simple Mendelian dominant in crosses with other species. In the history of its origin it forms an exact parallel to *Œnothera rubricalyx.* Cockerell (1915) has since studied many elementary forms in the wild species. He quotes from Church the history of the cultivated *H. annuus,* L. which is a gigantic non-branching form. Like maize, its origin in cultivation is only a matter of conjecture. Its seeds furnished the oil supply of pre-Columbian America, and apparently it is a product of Peruvian agriculture. It is very likely a gigantic form of some unknown species perhaps native of Mexico. Its cells should be examined, and their size compared with the cells of other species. Its relation to *H. tuberosus,* the girasole or Jerusalem artichoke, another Indian food plant, is also a matter of interest. In the latter species Cockerell (1919) has described a number of varieties, in cultivation and possible mutations in the shape of tuber, including *multituberculatus, fusiformis, purpurens* and *purpurellus.*

THE MECHANISM OF ROOT PRESSURE.[1]

By J. H. Priestley.

[With Two Figures in the Text.]

Introduction.

AN attempt is made in the following paper to give an explanation of the mechanism of root pressure that shall be in accord with the experimental evidence and with physics and chemistry.

Most of the data presented below are drawn from the work of other investigators, and additional experimental work has only been referred to occasionally where it supplied further evidence for the views advanced.

There is, therefore, little that is new presented below; at the same time it is thought that most of these facts have not been marshalled before as a basis for an explanation of the mechanism of root pressure, and it is hoped that their treatment from this point of view is justified by the satisfactory basis upon which it places this subject.

Arising out of the views stated below, a large amount of experimental work is in progress in this laboratory, and it may be said at once that the work, which it is hoped to publish later, in no way clashes with the theoretical considerations advanced below as to the mechanism of root pressure.

Osmosis is obviously of primary importance in connection with the process by which sap is driven up the xylem from the roots, and, with the aid of Text-fig. 1, an attempt will be made to estimate the significance of osmosis in this process.

In the diagrammatic section of a young root shown in Text-fig. 1, it is permissible to consider all the cells in the series, from the root-hair A to the cell L, bordering upon the xylem vessel, as having cellulose walls, permeable to water and the majority of solutes, and as lined with a layer of living protoplasm, which functions as a semi-permeable membrane. These cells frequently have starch stored within them, and presumably, therefore, sugar is present dissolved in the cell sap. If this sugar is brought down from the leaves by the vascular strands it will tend to be more concentrated in the sap of L, but whatever may be the original concentration in these cells, owing to the entry of water from the

[1] The substance of this paper was communicated to Section K of the British Association, Bournemouth Meeting, September, 1919.

soil solution into the root hair A, a gradient will soon be established in which the concentration of the solutes in the sap of L is greater than in the sap of K, which is greater than in the sap of J, etc.

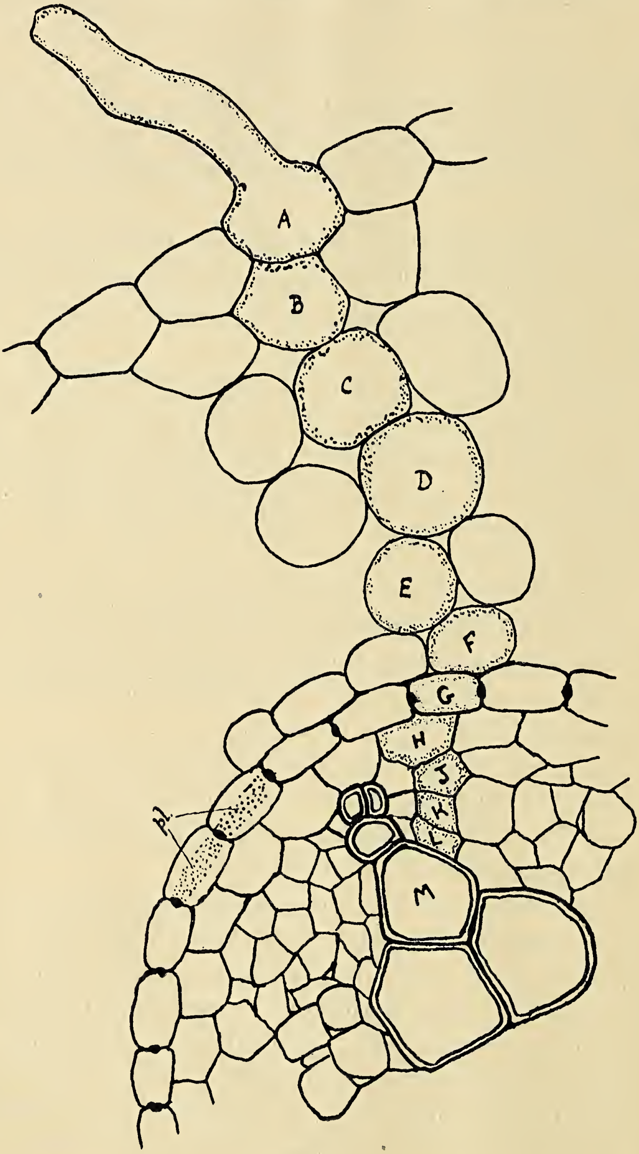

Fig. 1.

As a result of an osmotic gradient of this nature water will be entering the cells of the periphery of the root and passing towards the centre where it will gradually distend the cells of the tightly packed parenchyma within the vascular cylinder.

We can then understand the passage inwards of the water from the surface of the root to cells in the position of L, Text-fig. 1, but the further passage of the water into the cavity of the xylem vessel seems at first sight to present a difficulty. The cellulose wall of L is completely lined within by the usual semi-permeable layer of protoplasm, whilst M has no such lining. Under these conditions, unless the sap within M contains a sufficient concentration of solutes to be in osmotic equilibrium with the cell sap of L, water will apparently be withdrawn from M to L by osmosis. But if the cell sap of L is under sufficient pressure, the sap may remain in equilibrium with a more dilute solution in M, which, protected by its rigid lignified wall, is not under the same pressure. Gelston Atkins (1, loc. cit. p. 201) has, in reality, invoked this explanation when suggesting that the ascent of water in the xylem of the root may be explained as an osmotic phenomenon, acting from the dilute sugar solution in the xylem to the soil solution outside, through a mass of living cells, *treated as one semi-permeable membrane.*

The parenchyma within the endodermis, *e.g.*, the cells H, J, K, L, are confined within an endodermis, the extensibility of which is limited, the radial walls of the cells being clamped by lignified thickenings; and frequently the other walls of the endodermal cells are also greatly strengthened.

No air spaces are present between the cells, and the walls of the xylem vessel are rigid. Between endodermis and xylem vessel, the cells then are practically unable to expand, and under these conditions it is physically possible to have the internal hydrostatic pressure, within cells in the position of L, so high that water may be forced into M, although the solution in M has a lower osmotic pressure than the cell sap of L.

The function of the endodermis in this process will now be considered more closely, but it must first be pointed out that the hydrostatic pressure exhibited by the cells from H to L will not alone explain the continuous rise of water in the xylem vessel M, although it would explain the sap in L remaining in equilibrium with a less concentrated solution in M. M would have to retain a very appreciable osmotic pressure, and, as M contains no living protoplasmic contents, the only conditions under which this would seem possible, would be under circumstances which would permit of a constant supply of solutes to M from the adjacent cells. The phenomena investigated by Lepeschkin in the excretion of water by hydathodes seem to throw light upon this question.

To understand the possible mechanism by which the water in L can be continually supplied to M, it will therefore be necessary to discuss two questions, (1) the significance of the endodermis, (2) the excretion of water by superficial hydathodes.

The endodermis. As the water passes inwards from the cortex of the root the endodermis is the first continuous, unbroken layer of cells encountered (a somewhat similar layer may be present near the exterior of the root in the form of an exodermis and possibly its function may be interpreted upon somewhat similar lines to those adopted in the subsequent discussion upon the functions of the endodermis).

The continuous layer of endodermis in a young and functional root encloses a core of tissue in which parenchyma, sieve tubes and xylem vessels are tightly packed without intervening air-spaces.

A very characteristic feature of the endodermis is the thickening of the radial walls, which usually have the same staining reactions as the lignified xylem walls, but this radial thickening is not itself merely lignified. On the contrary, there is very considerable evidence (Haberlandt, 6, loc. cit. pp. 368, et seq.) that this radial thickening is suberised and impermeable to water. The same thickening of the radial wall is visible in longitudinal sections of the root and it is easy to establish that this impermeable strip is continuous all round the radial transverse and radial longitudinal walls of the cell.

This means that, as the water passes from the cortex of the root into the central core through the cylinder of endodermis, it cannot follow a path across the endodermis such that it remains always in the wall, it must enter the protoplasm.

De Rufz de Lavison (4, 1911) has brought out this point very clearly. He has shown that even when the cells are vigorously plasmolysed, the protoplasm is not withdrawn from the suberised strip, the plasmolysed protoplast always taking the form shown at 'pl' in Text-fig. 1.

De Rufz de Lavison (3, 1910 and 4, 1911) has also shown that solutes in the water surrounding the root, if unable to penetrate the protoplasm, can diffuse into the root as far as the endodermis, diffusing inwards by the walls, but they are then completely stopped at the endodermis. Similarly if the root tips are cut across, and the cut ends dipped into water so that this is then drawn up through the xylem by the ascending current due to transpiration from the leaves, if the ascending water currents contain a substance, incapable of penetrating the protoplasm, but whose passage through

the walls can be followed by its colour or by subsequent staining reactions, then this substance will be traced diffusing outwards as far as the endodermis and no further. These experiments of De Rufz de Lavison seem very conclusive, and quite similar results have been obtained by the writer, but are not described in detail as De Lavison's papers are readily accessible.

De Lavison (3, loc. cit. 1910), likewise Haberlandt (6, loc. cit. pp. 371, 372) refers to experimental work of de Vries (10, 1886) not accessible in the original to the present writer. In these experiments de Vries apparently found that if he forced water into the root from the surface of the cut stem it was impossible to obtain a leakage of this water from the root unless the endodermis was injured. Presumably a pressure was never used which exceeded in magnitude the opposing osmotic pressure retaining the water within the protoplasts of the endodermal cells.

The above facts taken in conjunction lead then to the conclusion that water, in passing through the endodermal cylinder, must pass through the protoplasts. As the considerations studied previously show that these protoplasts find themselves linked in a series of cells in which the osmotic gradient rises towards the inside, this is tantamount to saying that under normal conditions the passage of water through the endodermis is completely controlled by osmotic phenomena, and is always taking place in an inward direction. Before considering the further bearing of these facts we will discuss the significance of some modern work on the excretion by hydathodes.

(2) *Excretion by hydathodes.* The hydathode is one special case, dealt with by Lepeschkin (8, 1906) in his study of the excretion of water by plants.

For details reference must be made to the original papers; for present purposes, it is sufficient to cite the facts as to the excretion of water by the multicellular hair of *Phaseolus multiflorus.* (Fig. 2.)

On the basis of his experimental results with the young sporangiophore of Pilobolus, Lepeschkin explains the continuous excretion of water from the two top cells of this hair by the assumption of a different semi-permeability of the protoplasmic layer on the upper, as compared with lower, side of the cell.

If this protoplasmic layer is more permeable on the upper side, then before the internal hydrostatic pressure arrives at the level that it is possible to obtain through the entry of water at the lower side of the cell, water *and certain solutes* will be passing out of the cell at the top on to the upper surface. This excretion of water

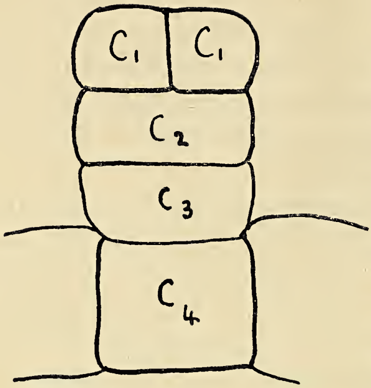

Fig. 2. Diagram of multicellular hydathode of *Phaseolus multiflorus.*

Text-fig. 2 represents sufficiently the conditions prevailing in one of these excretory hairs, where we have a series of cells with permeable cellulose walls, lined by semi-permeable protoplasmic membranes, and with internal osmotic concentrations such that C4 is less than C3 is less than C2 is less than C1, but C4 is greater than the osmotic concentrations of the epidermal and mesophyll cells surrounding it.[1] and solutes will continue so long as there are sufficient solutes to maintain C1 higher than C2 and also high enough to generate a hydrostatic pressure sufficient to force water and solutes through the upper surface of the cell. It is important to notice that in a hydathode functioning in this manner (compare the hydathodes of *Colocasia anti-quorum*, see p. 198) the excretion, if arising from the causes explained above, will never be pure water. In fact it is difficult to see how the excretion of pure water under such conditions could be harmonised with thermodynamics; water would be moved and work done, apparently without energy being expended, as the osmotic concentration within the cell would then remain unaltered.

The solutes in the excretion were usually inorganic. Lepeschkin found for example, the following percentages of inorganic ash in the excretions from superficial cells of the plants named :—*Phaseolus* 0·4%, *Abutilon* 0·5%, *Nicotiana* 0·1%, *Polypodium* 0·2%, *Camellia* 0·5%, *Lathyrus* 0·5%. He found organic substances in the excretions in the following cases ;—*Lathyrus odoratus* (alkali salts of organic acids); *Vicia sativa* and *Polypodium aureum* (glucose). The excretion was alkaline, except in the case of *Lathyrus*. $CaHCO_3$ was usually present in a relatively large proportion amongst the inorganic salts.

Returning to our present problem of root pressure, it will readily be seen how the data cited above enable us to fashion a hypothesis to overcome our difficulty of the passage of water from the cells (as L, Text-fig. 1) bordering on the xylem vessels, into the xylem vessels.

[1] Bayliss (2 loc. cit. p. 163) describes the osmotic concentration in these hairs as decreasing from base to apex, but undoubtedly he has quoted Lepeschkin incorrectly.

Throughout all the mass of parenchyma, packed between the rigid xylem tubes of the centre and the relatively rigid (frequently strongly lignified) outer cylinder of endodermis, a strong hydrostatic pressure is developing owing to the entrance of water, governed by the existing osmotic gradient. Cells such as G (Text-fig. 1) are in the position of the basal cells of the hydathode (with concentration C4, Text-fig. 2), cells such as L (Text-fig. 1) are equivalent to the apical cells of highest osmotic concentration (C_1, Text-fig. 2). If then, we make the same assumption as Lepeschkin, and assume that the protoplasmic membrane of L, as it abuts upon the xylem, is of relatively greater permeability than the protoplasmic layer of L where it abuts on other parenchymatous cells,[1] then we have the conditions existing for an excretion of water, *plus solutes*, into the xylem vessel so long as the osmotic pressure in L is greater than the osmotic pressure in K, and so long as the hydrostatic pressure generated within the core of tissue within the endodermis is strong enough to force water and solutes into the xylem vessel from L.

When this stream of water and solutes enters the xylem vessel M, the only direction in which it is free to move is upwards in the cavity of the vessel. It is true it may leak through permeable cellulose walls, around the protoplasts, back as far as the endodermis, but at the endodermis it meets the barrier of the suberised region and cannot leak outwards any further (see page 4).

At this point it is necessary to refer to a few simple experiments which support the hypothesis outlined in the preceding paragraphs.

It would appear at first sight that even if water may not leak outwards from the xylem vessel to the surface because of the suberised walls of the endodermis, a slight leak might occur near the root tip where the endodermal cylinder is not yet differentiated. Such a leak would probably in any case be a minor factor, as the *walls* of the cells in the apical region, through which alone this leakage could take place, are very thin and the outward diffusion under the existing pressure through their total cross section would be small. But as the result of a number of experiments in this laboratory with various readily penetrating dyes, it is suggested that even this amount of leakage probably does not take place. As stated previously, de Rufz de Lavison's observations that such

[1] For this difference in permeability good structural cause may well exist. The ectoplasm in one case will be supported by a similar layer opposed to it, to which it is attached by protoplasmic connexions, in the other case the ectoplasm faces a "dead" lignified layer.

a dye, if it cannot penetrate the protoplasm, does not penetrate through the walls further inwards than the endodermis have been confirmed. In the course of these experiments it was noted that at the root tip the penetration inwards via the walls was even less marked. To obtain the result it is necessary to experiment with roots that have been previously grown in water: otherwise, when the roots are transferred to the dye solution toxic conditions are invariably produced and the dye penetrates right through the tip, freely entering the dead cells.

These observations have been made on willow roots and onion roots, using various dyes chosen for their penetrability on the basis of the valuable data given by Ruhland (9, 1912). Good results have been obtained with light green FS, orange G, neutral red and malachite green.

These dyes penetrate cellulose walls readily and in some cases can penetrate the living protoplasm. Their inability to penetrate at the root tip suggests, therefore, that the cell walls in the neighbourhood of the apex have the properties of protoplasm rather than of dead cellulose walls, at any rate with regard to diffusion. By the use of such dyes it is also possible to obtain ready confirmation of the greater permeability of the apical cells of the hydathodes of *Phaseolus vulgaris*. If a leaf of this plant be dipped in dilute (0·05%) aqueous neutral red, for a few hours, and then a section of the leaf is examined in water, the plasma of the apical cells of the hydathode will be found to be deeply stained, but the lower cells of the stalk will not be stained even after 24 hours' immersion.

That some of the cells within the endodermis likewise have a greater permeability relatively to the endodermal cells, has been illustrated by similar experiments, so that these cells correspond in this respect to the apical cells of the hydathode and the endodermal cells to the basal cells. In these experiments young plants are taken and their root tips cut across under water and the roots then placed in aqueous solutions of various dyes (usually 0·1%). Best results have been obtained with acid green, malachite green, neutral red, and light green FS. But various seedlings may be used and probably the exact combination of seedling and dye for best results varies with different external conditions. The solution of the dye is then drawn up the xylem and the water previously inside the vessels is drawn up to the leaves to replace that lost by transpiration.

If a section is cut across the root some 24 hours later, the walls of the xylem will be found to be stained, and possibly the dye will have diffused via the walls as far as the endodermis, any patches of thick walled sclerenchyma within the endodermis being thus quite likely to show their walls well stained. But the protoplasts within the cells will still be quite colourless, except for some cells close to the xylem, but not always immediately adjacent. Frequently these cells form a group lying between protoxylem and endodermis. These cells will stain deeply and show up most conspicuously, owing to the fact that the dye has in many cases penetrated them and accumulated within them. The effect has been particularly well seen in this laboratory, using acid green and seedlings of *Vicia Faba.*

It is submitted then that the hypothesis outlined above, based on the work of other investigators and supported by a small amount of new experimental evidence, provides an adequate basis for the interpretation of the phenomenon of root pressure. It is not pretended, however, that the hypothesis is free from difficulties and one or two of these will now be briefly considered.

One outstanding difficulty in the case of a hydathode which functions for some considerable period, is accentuated in the case of the root where a very considerable stream of water may pass upwards. It is difficult to understand how the necessary solutes can be provided in sufficient quantity to permit of the constant leakage of the solute across the inner membrane of cells such as L. (Text-fig. I).

From Lepeschkin's work, such solutes might be either organic or inorganic. It is suggested tentatively that in the root they are organic, and either sugars, or, more probably, organic acids derived from the breaking down of sugars. Of these sugars probably a constant supply is available from hydrolysis of the stored starch or from the sugars arriving by translocation from the leaf. In favour of the view that the solute is a sugar may be quoted the data given by Gelston Atkins (I, loc. cit. Chap. XI) as to the presence of sugar in the sap rising in the xylem, and the interesting data as to the permeability of blood corpuscles to glucose, discussed by Bayliss (2, loc. cit. pp. 126 and 127) which leads him to the conclusion that "The facts suggest the possibility that the normal semi-permeability of the membrane to glucose is connected with a particular difference of concentration on the two sides, but that the actual value of this difference may be changed by other influences."

This conclusion of Bayliss leads to another consideration it may be well to keep in mind. If the permeability of a protoplasmic membrane to glucose is a function of the difference of concentration on the two sides of the membrane, then the accumulation of sugar within L, or the dilution of this sugar by entrance of water, might be factors leading to a change in the permeability of the protoplasmic membrane on the side bordering on the xylem vessel, and such a change might have the result of rendering the membrane on this side *temporarily* permeable to sugar. In other words, instead of the constant excretion of water, noted by Lepeschkin in the hydathodes under observation, we may here be dealing with an intermittent phenomenon in which changes in permeability follow upon the changes in concentration within the protoplasts bordering upon the xylem, the original permeability, or lack of permeability, being restored as these concentrations readjust themselves by temporary discharge of water and solute into the xylem stream. This process, intermittent in the individual cell, would appear as a continuous process in the phenomenon of root pressure, where the final result is the sum of the activities of many thousands of cells in different phases of activity.

Returning from this digression to the problem as to the constant provision of the solute which passes out with the water into the xylem vessel, the hypothesis that this solute is an organic acid derived from sugar has much attractiveness. As pointed out by Bayliss (2, loc. cit. p. 165), such chemical changes permit of rapid increase in the osmotic concentration, one molecule of glucose giving rise to several molecules of acid. Futhermore, the experimental data already accumulated (see for instance Hind 7, 1914, p. 229, et. seq.) show that protoplasm is relatively rapidly permeable by organic acids under some conditions, though the facts of translocation drive us to assume a similar permeability for sugars under certain unknown conditions.

Another difficulty is the apparent contradiction between the assumption that solutes enter the xylem vessel with the water of the root pressure stream, and the facts recorded by Flood (5, 1919) in the case of the excretion from the leaf tips of *Colocasia antiquorum*. This very vigorous excretion has been shown to be due to the activity of the roots in pumping water up, and, during its upward passage until its exit at the tip, the water passes through no filtration mechanism whatever. But the water excreted is practically free from impurities. In that case what becomes of the

assumption that solutes must enter the xylem vessel from the secreting cells in the root?

The assumption and the factor are probably reconcilable, on the grounds that after excretion and during the subsequent upward passage in the xylem the ascending stream is always in contact through the xylem walls with the surrounding protoplasts. Under these circumstances, physical adsorption on the surfaces limiting the stream may well be followed by physiological absorption, whether the solutes in the ascending stream are organic or inorganic, sugars or acids.

This suggestion must probably appear in any theory of root pressure, because the fundamental tenets of thermodynamics seem difficult to reconcile with any other assumption than the original excretion of solutes with the water into the xylem vessel.

It is not claimed that this discussion is exhaustive, but it is submitted that the account of the mechanism of root pressure given above fairly states the difficulties and provides, with the minimum of assumption, a hypothesis, founded chiefly on observation and experiment, that is adequate to account for the facts.

This hypothesis should be of interest because on the one hand it suggests the revision of anatomical data with reference to the endodermis to see if they will permit this interpretation of its function and on the other it points the way to a series of physiological investigations which may throw further light on the phenomena of permeability.

It is hoped to give a more detailed account later of the experimental work arising out of the views stated above, and with such an account other names would be associated. In connexion with the experimental work briefly touched upon above, I have to acknowledge the help of Miss D. Armstead, Research Assistant in the Department, and of Miss Tupper Carey. I should also like to express my great obligation to Dr. S. A. Shorter, for his patient assistance in helping me to struggle towards enlightenment on the physical side of the problem.

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REFERENCES.

1. Atkins, W. R. G. Some recent researches in Plant Physiology, Whittaker & Co., 1916.

2. Bayliss, W. M. Principles of General Physiology, Longmans, Green & Co., 1915.

3. De Rufz de Lavison, Jean. Du mode de pénétration de quelques sels dans la plante vivante. Role de l'endoderme. Révue General de Botanique, Vol. 22, p. 225, 1910.

4. De Rufz de Lavison, Jean. Recherches sur la penetration des sels dans le protoplasme et sur la nature de leur action toxique. Ann. des Sci. Nat Bot. 9e Serie XIV, pp. 97-189, 1911.

5. Flood, Margaret. Exudation of Water by Colocasia antiquorum. Proceedings of the Royal Dublin Society XV, (N.S.) No. 36, April, 1919.

6. Haberlandt, G. Physiological Plant Anatomy, translated by Montagu Drummond. Macmillan & Co., 1914.

7. Hind, Mildred. Studies in Permeability III. The absorption of acids by Plant Tissue. Annals of Botany 30, 223 238, 1916.

8. Lepeschkin, W. W. Zur Kenntnis des Mechanismus der aktiven Wasserausscheidung der Pflanzen. Beihefte zur Bot. Centralblatt, XIX (1), p. 409, 1906.

9. Ruhland, W. Studien über die Aufnahme von Kolloiden durch die pflanzliche Plasmahaut. Jahrb. für Wissensch. Bot. 51, 376-431, 1912.

10. De Vries. Studien over Zuigwortels. Maandbl. vor Natuurwetensch Bd. XIII. 53-86, 1886. Abstract in Bot. Zeitung, p. 788, 1886.

METHODS AND SIGNIFICANT RELATIONS IN THE QUANTITATIVE ANALYSIS OF PLANT GROWTH.

By C. West, G. E. Briggs, and F. Kidd.

THE present authors are conducting a comprehensive study of the growth of *Helianthus* and are publishing (4) the results they have obtained from an analysis of the huge mass of data presented in the literature nearly half a century ago by Kreusler and his co-workers (7). It has been brought home to them very clearly in the course of this work that the previous attempts to express growth by some simplified formula are based upon a superficial similarity or upon wrong assumptions.[1] The effect of such generalisations has been to give an air of finality and to divert attention from the possibilities of deeper analysis. It is the formulation of methods for such an analysis that appears to us most urgent at present, and we have thought that it would be of interest to put forward at this stage the data and relations that seem to us significant.

The Unit of Measure.

In considering the problem of plant growth the plant physiologist is faced with the question as to what unit of measure he shall adopt. From whatever point of view the growth of a plant

[1] For a more detailed consideration and criticism of these formulæ the reader is referred to (4).

as an organism be considered, growth appears most broadly speaking as a process of increment in dry-weight. Accordingly, in line with the practice of previous investigators in this branch of plant physiology increase in dry-weight may be adopted as the best measure of growth.

The Study of Growth Rates as opposed to the Study of Final Yields.

Until recently the idea of rates as applied to the growth of the plant as a whole has been only vaguely conceived. Investigators, especially those working along economic lines, have been concerned mainly with the final yields. A study of plant growth from the outlook of rate is, however, more fundamental in so far that it aims at disentangling the details of the mechanism of growth and at a precise knowledge of the factors limiting growth throughout its course.

A solution of the problems of growth may be regarded primarily as the precise determination and evaluation of those factors, internal and external, which control the *rate* of the plant's increase in dry-weight from time to time throughout its life-cycle. Secondarily, after these factors are known and their values expressed in appropriate units, we may be in a position to state constants for the growth-rate of particular plants applicable to the whole life-cycle, and such constants will not only be of use from the economic point of view in comparing plants, but also will have physiological significance.

A rate is the amount of change per unit time. The actual rate of growth is the increase in dry-weight per unit time and depends upon various external factors and upon what we may call the amount of the "growing material."[1]

Growth Rate expressed per Unit of Dry Weight.

It is clear that if we could determine the unit of "growing material" it would be possible to express the rate of growth per unit of "growing material," and we should then be in a position to evaluate the various external factors and to determine specific plant constants. Under constant external conditions the rate so expressed would remain constant for a given plant, and changes in rate observed would be related to changes in external factors when these factors are limiting the rate. Let us take the simple case of a population of unicellular organisms growing in a medium the composition of which, together with other environmental factors, is constant. In such a case the actual rate of growth, as

[1] The term "amount of growing material" is equivalent to the 'active mass' of the reactant in a chemical reaction.

measured by the size of the population or its dry-weight, is found to increase exponentially with time, but the rate per unit of population or per unit of dry-weight is constant throughout (14). We may, therefore, legitimately take the dry-weight at any moment as a measure of the material actually engaged in growth at that moment and proceed at once to the determination of a growth constant.

In this simple case the method of expressing the rate of growth is physiologically sound in so far as the rate remains constant under constant conditions, and changes in rate would be expressions of changes in environment. The soundness of the method depends upon the fact that all the material is equally active in forming new growth by cell-division and by assimilation of new material, and hence the dry-weight of any time is a measure of the material responsible for dry-weight increment and growth.[1]

In the higher plants the state of affairs is more complex. The material of the plant is not all equally active in forming new growth by cell-division and by assimilation, and moreover we do not know that the relation of the amount of material actually engaged in growth to the total material (dry-weight) is constant: in fact the evidence from morphological considerations and from analyses of growth data carried out by the present writers (4) is that the relation undergoes a definite type of variation. Consequently, in relating growth to dry-weight in the higher plants we are not relating growth to the amount of actual "growing material." The growth-rate expressed per unit of dry-weight does not remain constant under constant external conditions and we cannot therefore, on this basis alone, determine constants for the plant, nor can we evaluate the effect of environmental factors.

Previous Attempts to evaluate Constants for Plant Growth.

In practically all previous attempts to evaluate constants for plant growth the rate, *i.e.*, increase in dry-weight per unit time, has been expressed per unit of dry-weight. The formula $\frac{dx}{dt}=Kx\ (A-x)$, or in its integrated form $\log\frac{A-x}{x}=K\ (t-t')$, which is the autocatalytic formula put forward by Robertson (12 & 13) as expressing the growth of an organism, and which Reed (8 & 9) and Rippel (10 & 11) apply to the growth of the plant organism, involves the assumption that since K is constant,[2] x, the dry-weight, is a measure of the "grow-

[1] The result is actually a statistical one, assimilation preceding cell-division in the individual, but at any moment both processes are going on when the population as a whole is considered.

[2] Reed goes as far as to assume that K is a constant apart from A.

ing material" and also that the rate per unit of "growing material" decreases throughout the life cycle owing to the disappearance of a catalyst as growth proceeds. Such a formula, which fits the facts only approximately and explains the falling off in rate per unit dry-weight as being due to the disappearance of a catalyst, obviously does not help us much in an analysis of plant growth, and we agree with Enriques (5) that the similarity between an autocatalytic reaction and the growth of a plant is a purely superficial one, the falling off in rate per unit dry-weight being due rather to increasing differentation into productive and non-productive tissues.

The formula $\frac{dW}{dt}=rW$, or in its integrated form $W=W_0e^{rt}$, originally put forward by V. H. Blackman (1) with the idea that it was an important physiological constant, involves the assumption that dry-weight (W) is a measure of "growing material." It has been shown that the rate per unit dry-weight, r, is not a constant (3 & 6).

Suggested Procedure in the Study of Growth Rate.

Before we can determine constants for a plant which have any physiological significance and which are comparable with physico-chemical constants we require a much more detailed analysis of the growth throughout the whole life-cycle. To this end we consider that the best procedure is to calculate the rates in relation to various units of the plant from data collected at frequent intervals. In this way we obtain a number of parallel records of rates throughout the life-cycle. By a careful comparison of these with each other and with the records of environmental factors we may hope to disentangle the problems of plant growth and proceed to the evaluation of constants. More in detail our technique and terminology are as follows:—

(1). *Primary Data.* Measurements of dry-weight and leaf-area at intervals of a week or less accompanied by measurements of respiration, assimilation, transpiration and chemical analysis of the plant tissue, and continuous records of the various environmental factors likely to affect growth. In order that these data when collected may be of real value it is necessary to adopt a sound statistical procedure, *e.g.*, utilisation of material as uniform as possible, large samples and calculation of probable errors.

(2). *Significant Secondary Relations.* The presentation of the results so obtained through the complete life-cycle in four series of numbers which can, if desired, be put in the form of graphs— "*Relative Growth Rate*," "*Leaf Area Ratio*," "*Unit Leaf Rate*" and "*Relative Leaf Growth Rate*."

The *Relative Growth Rate*, R, is the weekly percentage rate at which the dry-weight increases. It may be assumed for purposes of calculation that the increase from week to week takes place exponentially, R being the exponent, or that it takes place linearly. Both are approximations. As to the relative merits of the two different methods the reader is referred to (4). If R be the *Relative Growth Rate* and W the dry weight then $\frac{dW}{dt}=\frac{RW}{100}$. This formula expresses the relation between R and W assuming the increase takes place exponentially and when integrated the equation becomes $\log_e W_2 - \log_e W_1 = \frac{R}{100}$, where W_2 is the dry-weight at the end of the week, W_1 the dry-weight at the beginning of the week and e the base of the natural logarithms. If it is assumed that the increase is linear $\frac{R}{100}=\frac{W_2-W_1}{W_1}$.

By *Leaf Area Ratio*, A, is meant the ratio of leaf-area to dry-weight, that is $\frac{L}{W}$. For simplicity $\frac{\frac{L_1+L_2}{2}}{W_1}$ is used when making calculations on the linear basis, L_1 being the leaf-area at the beginning of the week and L_2 at the end of the week.

By *Unit Leaf Rate*, E, is meant the weekly rate of increase in dry-weight per *Unit Leaf Area.*[1] Then $\frac{dW}{dt}=EL$, and if the exponential basis be adopted for both leaf-area and dry-weight increase, then $E=(\log_e L_2 - \log_e L_1)\ \frac{W_2-W_1}{L_2-L_1}$. On the linear basis for leaf-area $E = \frac{W_2-W_1}{\frac{L_1+L_2}{2}}$, that is, the weekly increase in dry weight divided by the Average Leaf Area.

Relative Leaf Growth Rate, R_L, is analogous to Relative Growth Rate and $\frac{R_L}{100}=\log_e L_2 - \log_e L_1$, or $\frac{L_2-L_1}{L_1}$ according to whether the calculations assume an increase on the exponential or on the linear basis.

An inspection of the above definitions and formulæ will show that whichever formal conception as to the mode of increase of dry-weight and leaf-area be adopted the Relative Growth Rate is merely the product of the Leaf Area Ratio and the Unit Leaf

[1] Cf. Weber's "Specifische Assimilationsenergie" (15).

Rate multiplied by 100. This will be made clear by the following. On the exponential basis $R = \frac{100 \frac{dW}{dt}}{W}$, $A = \frac{L}{W}$ and $E = \frac{\frac{dW}{dt}}{L}$ and hence R=100A.E. On the simple interest basis it will be seen that the same relationship holds. None of the above formulæ involve the assumption that R, R_L, A or E are constant throughout the life-cycle.

An examination of data shows that in the early part of the plant growth the increment of dry-weight and of leaf-area is more or less exponential, whilst later it approaches to being linear. Thus in order that the calculated rates may approximate more closely to accuracy, especially in the case of the Unit Leaf Rate, the exponential basis should be adopted in the early period whilst in the later period it makes little difference in the calculated rate which basis of calculation be adopted. The importance of obtaining values for Unit Leaf Rate which approach closely to accuracy is that these values may be compared with values of assimilation determined by gasometric and half-leaf methods.

Our reason for adopting Unit Leaf Rate as a significant relation in the analysis of plant growth is that we have at our disposal a certain amount of definite knowledge with regard to the effect of environmental factors upon assimilation. By making the necessary allowances for variations in environmental factors we can determine to what extent assimilation controls growth and to what extent it is controlled by growth.

Another problem which can be attacked by the above method is as to how far differences in *Relative Growth Rate* of different plants are due to differences in *Unit Leaf Rate* and how far to differences in *Leaf Area Ratio.* This problem is now under experimental investigation by the authors.

In the case of maize the ratio of productive to total weight is not constant but the *Relative Growth Rate* and *Leaf Area Ratio* undergo similar and simultaneous variations, thus suggesting that *Unit Leaf Rate* is roughly constant throughout the main parts of the plant's life-cycle, and that, considering the growth of a plant as analogous to money accumulating interest, the leaf-area is a better measure of capital than is the dry-weight.

The above suggestions are to be considered simply as proposals for formal methods of assembling secondary data on what appear to be the most profitable lines as a result of the closest inspection possible at present. It is to be emphasised that

the relations it is proposed to record at weekly intervals throughout the life of a plant do not involve any general presumptions as to the factors controlling growth as a whole, such, for example, as the presumption that growth is controlled by assimilation or that growth is controlled by root absorption. Our attitude is that general conclusions should be postponed until sufficient secondary data, based on sound primary data, have been carefully analysed. From the primary data mentioned above other secondary data in addition to those proposed by us can obviously be obtained, and as analysis proceeds it is possible that some of such further relations may be found to be significant in finally arriving at conclusions with regard to the various factors controlling growth.

The quantitative analysis of plant growth week by week by some such method as that outlined has not been carried out before, and we have been influenced in putting forward our tentative suggestions by the hope that they will stimulate and be of use in further research. It is obvious that it would be a distinct advantage if various workers on this problem would make use of the same general methods or at least present their results not only in graphical form but also by giving the actual figures obtained. It is much to be regretted that such a contribution to the subject as that of Brenchley (3) is devoid of any primary data whatever concerning the plants themselves.

Botany School, Cambridge. *June, 1920.*

NOTE.

In reply to a suggestion put forward by us in the previous number of this journal (6) to the effect that from an economic point of view the "substanzquotient" is preferable to the "efficiency index" in that it only states the ratio of final weight to seed weight divided by time and makes no assumption as to the rate of addition of dry material, Professor V. H. Blackman (2, p. 99) states that "a formula in which final weight is divided by seed weight and by time implies that there is a linear relation between time and weight." This would have been the case if we had said that the "substanzquotient" was a constant, but we stressed the point that the "substanzquotient" varied with time and hence had no physiological significance.

LITERATURE CITED.

1 Blackman, V. H. The Compound Interest Law and Plant Growth. Ann. of Bot., XXXIII, 1919, p. 353.

2. ,, ,, The Significance of the Efficiency Index of Plant Growth. New Phyt., XIX, Nos. 3 & 4, 1920, p. 97.

3. Brenchley, W. E. On the Relations between Growth and the Environmental Conditions of Temperature and Bright Sunshine. Ann. Appl. Biol., VI, No. 4, 1920, p. 211.

4. Briggs, G. E., Kidd, F. and West, C. Quantitative Analysis of Plant Growth. Ann. Appl. Biol., VII, 1920. (In the Press).

5. Enriques, P. Wachsthum und seine analytische Darstellung. Biol. Centralbl., 1909, p. 337.

6. Kidd, F., West, C. and Briggs, G. E. What is the Significance of the Efficiency Index of Plant Growth? New Phyt., XIX, No. 3 & 4, 1920, p. 88.

7. Kreusler, U. et al. Several papers on the growth of crop plants in Landw. Jahrb., 1875-85 inclusive.

8. Reed, H. S. and Holland, R. H. The Growth Rate of an Annual Plant *Helianthus*. Proc. Nat. Acad. Sc., U.S.A., V, No. 4, 1919, p. 135.

9. Reed, H. S. The Nature of the Growth Rate. Journ. Gen. Physiol., II, No. 5, 1920.

10. Rippel, A. Die Wachstumskurve der Pflanzen und ihre mathematische Behandlung durch Robertson und Mitscherlich, Fühlings Landw. Zeit., LXVIII, Heft 11/12, 1919, p. 201.

11. Rippel, A. Die Wachstumskurve, Ber. d. deutsch. bot. Gesellsch., XXXVII, Heft 3, 1919, p. 169.

12. Robertson, T. B. Further Remarks on the Normal Rate of Growth of an Individual, and its Biochemical Significance. Archiv. f. Entwickelungsmechanik, XXVI, 1908. p. 108.

13. ,, ,, On the Nature of the Autocatalyst of Growth. Archiv. f. Entwickelungsmechanik, XXXVII, 1913, p. 497.

14. Slator, A. The Rate of Fermentation by Growing Yeast Cells. Bioch. Journ. VII, 1913, p. 197.

15. Weber, C. Ueber specifische Assimilationsenergie. Arbeiten d. Bot. Instit. in Würzburg. Bd. II, Leipzig, 1882, p. 346.

PRELIMINARY NOTES ON ADDITIONAL EVIDENCE FOR THE HYDRION DIFFERENTIATION THEORY OF GEOTROPISM.

I.—On the Reversal of Geotropic Curvature in the Stem.

By J. Small and M. W. Rea.

SINCE the publication by one of us of a theory of geotropism supported by certain experiments (2) some considerable amount of additional evidence in favour of this theory has been obtained. The details of this evidence will not be published for some time, and therefore this preliminary account is being given.

The theory of the experiments is, briefly, that the differentiation in hydrion concentration in stem and root is caused by the comparatively slow escape of the CO_2 of respiration from the root, which thus becomes relatively acid; and the rapid elimination of that CO_2 from the stem and leaves either by diffusion through the stomata or by its utilisation in photosynthesis or by both these methods. The shoot therefore becomes relatively alkaline and the hydrion differentiation is in this way connected with the normal metabolism of the plant.

From this hypothesis it follows that when shoots are placed horizontally in the dark they may cease to react or may react in the reverse direction to the normal under geotropic stimulation. If these shoots are coated with vaseline the CO_2 of respiration should accumulate within and the geotropic response should be reversed.

Shoots of a number of very different plants have been treated in this way, *i.e.* coated with vaseline and placed horizontally in the dark. Most of the shoots so treated showed downward curvatures, while shoots left in the dark unvaselined in a number of cases showed upward curvatures and in others showed either no curvature or downward curvatures. The plants which showed reversed curvature include maize, *Pelargonium*, *Cerastium*, sycamore seedlings, *Myosotis* inflorescence, *Antirrhinum* seedlings, groundsel and *Anthemis*. No upward curvature or positive downward curvature in the dark has been observed in unvaselined specimens of maize, *Stellaria media* and sycamore seedlings. Photographic records of these experiments have been kept and we intend to give a detailed account when the problem of the CO_2 balance has been more thoroughly investigated. One point, however, should be noted. If the plants are placed horizontally in the dark immediately after

being vaselined they curve upwards as a rule. They must be placed vertically in the dark for two to seven days, to allow the CO_2 to accumulate, if downward curvature is to be demonstrated. In several cases recovery from downward curvature to upward curvature was obtained by placing the plants in the light, to enable them to remove the CO_2 by photosynthesis. The treatment with vaseline and darkness also inhibits the growth of the stem (cp. 1).

A practical application of the phenomenon which has just been described occurs in the "earthing-up" of potatoes; the "earthing-up" increases the amount of CO_2 in and around the lower stem branches with the result that they grow down into the soil and ultimately produce tubers, which may be regarded as physiological malformations due to the disturbance of the normal condition of the protoplasm. This explanation of the production of potato tubers may be extended to include the experience by farmers in the north of a loss in the potato crop, instead of a gain as with barley, when the plants are treated with high tension currents. To put the matter briefly—whereas the positivity of the high tension currents induces a negative charge in the already negatively polarised sub-aerial parts, that same positivity decreases the polarisation in the already positively polarised subterranean parts with consequent increase of permeability, loss of turgor, loss of growing power and decrease in tuber-production.

II.—On the Angle of Balance in Roots, Stems and Leaves.

By J. Small and M. J. Lynn.

In the above mentioned paper (2, p. 58, Fig. 5) an explanation, based upon the new theory of geotropism, is given of the orientation of secondary roots and stem branches. Certain deductions from that explanation are obvious. (1.) Provided that the distance of the point of junction from the tip of the main axis remains constant, the angle of balance will increase with the growth in length of the of the lateral organ, because the strength of the action current in it *at the point of junction* will decrease, and therefore a greater angle, giving a larger action current, will be required to balance the leak of the normal polarity current from the main axis. Since it has been shown (3, 4, 5) that the strength of the response (or action current) varies as the sine of the angle, it follows that when the angle of balance is plotted against the length of the lateral organ, the graph should be a sine curve. (2.) Provided that the length of the lateral organ remains constant, the angle of balance will

decrease with the growth in length of the main axis on the apical side of the point of junction, because the strength of the leak of the normal polarity current *at the point of junction* will decrease, and therefore a smaller angle, giving a smaller action current, will be required to balance that leak. These deductions are made with the additional hypotheses that the meristems of the lateral organs are more or less the same size in all the secondary roots *or* stem branches *or* leaves of the same species, and that the apical meristems of the main roots *or* stems are likewise constant within limits.

The angle of the lateral organ with the main axis would then vary directly as the length of the lateral and inversely as the distance of the point of junction from the apex of the main axis. If L be the length and D the distance, then the fraction L/D should vary as the sine of the angle.

Measurements have accordingly been made of the root-system of the pea, of the branch systems of the privet, cherry-laurel, *Rumex*, yellow cress and *Equisetum*, and of the leaves of *Pelargonium*, *Chrysanthemum*, *Rumex*, hazel and mint. The branches and roots have yielded curves which are similar within ten degrees either way to the sine curves for the angles found. The leaves have yielded similar curves which are, however, different in direction although not in kind. Superficial observations of many other herbs, shrubs and trees readily show that the same relations hold in them for both stem and leaf angles and lengths. This investigation is being continued and the detailed results will be given later.

III.—A Theory of the Origin of Leaves.

By J. Small.

In a recent account of the elements of phyllotaxis Church, referring to "the initiation of primary ramuli" says "One may not see exactly how it is done, as a more intimate plasmic or even 'molecular' function" (6, p. 56). The present contribution is an attempt to explain the missing point "how it is done" in so far as the higher plants are concerned, and the theory might be extended with certain modifications to the marine algæ of the phytobenthon.

In the above-mentioned paper (2) it is shown that the apical meristem of the shoot may be considered to be surrounded by circular zones of potential differences. The lateral organs, such as growing leaves, can be considered as possessing similar but excentric zones of potential differences. If the E.M.F. of the stem is small compared with that of the lateral organ we may compare

the electrical conditions to those which occur when a large bar magnet is placed horizontally near the opposite pole of a small erect cylindrical magnet. Then the lines of force can be demonstrated as arranged in Figure 1, with a small neutral area on the side of the "axis" magnet opposite or nearly opposite the bar magnet which takes the place of the lateral organ. It has been suggested that the polarisation of growth in the stem is due to the normal polarity current; the cells in that neutral area would, therefore, be freed from this polarising influence, and would grow out in all directions in the fundamental spherical form, giving the more or less hemispherical primordium of a leaf. The shape and size of the leaf primordium would depend upon the relative strengths of the two electric fields.

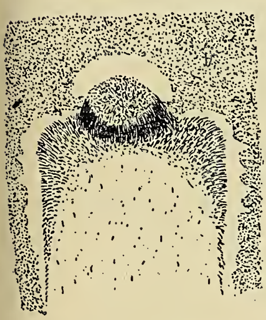

Fig. 1. Combined electric field of a large bar magnet and a small cylindrical magnet as shown by iron filings

Fig. 2. Combined electric field of one large bar and one smaller bar and one small cylindrical magnet.

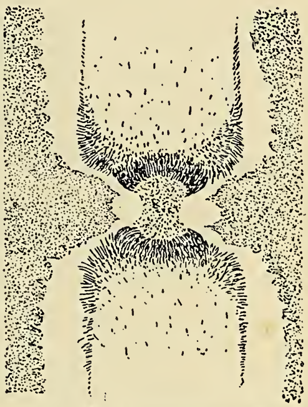

Fig. 3. Combined electric field of two equally large bar magnets and one small cylindrical magnet.

When the primordium has developed, an apical meristem is differentiated, with consequent loss of neutrality and acquirement of polarity, and a third electric field is developed (Fig. 2). The first leaf may be taken as the cotyledon, the second as a foliage leaf. The position of the third leaf or fourth electric field would then depend upon the rate at which growth caused the removal of the meristems of the first and second leaves away from that of the stem apex. Any slight inequalities of growth would result in tangential displacement, as in Fig. 2, and one primordium, not two primordia would be the result. Since these movements are part of a "continuous energy expansion system" (see 7, Chap. XX), the

arrangement on the ϕ ratio or spiral of Pheidias and the concomitant Fibonacci ratios are the natural consequences.

As a special case we have the opposite and decussate phyllotaxis (Fig. 3) where the lateral fields are equal in magnitude and in shape with the production of two equal, neutral areas arranged at right angles to the plane of the first two leaves. As these first leaves pass away by the elongation of the axis the primordia induced by them develop in their turn two electric fields which induce neutral areas and primordia directly above the first pair of leaves. These suggestions by analogy are being followed up and the results will be published later.

THE QUEEN'S UNIVERSITY OF BELFAST
June 16th, 1920.

REFERENCES.

1. Kidd, F. Laboratory Experiments on the Sprouting of Potatoes in various Gas Mixtures. NEW PHYTOLOGIST, XVIII, p. 248, 1919.
2. Small, J. A Theory of Geotropism. NEW PHYTOLOGIST, XIX, p. 49, 1920.
3. Fitting, H. Untersuchungen über geotropischen Reizvorgange Jahrbuch. f. wiss. Botanik, XLI, Teil I, p. 282. 1905.
4. Newcombe, F. C. Geotropic response at various angles of inclination. Ann. Bot. XIX, p. 311, 1905.
5. Small, J. Changes of Electrical Conductivity under Geotropic Stimulation. Proc. Roy. Soc., Lond. B, 90, p. 349, 1918.
6. Church, A. H. On the Interpretation of Phenomena of Phyllotaxis. Oxford Bot. Mem., No. 6, 1920.
7. Cook, T. A. The Curves of Life. Constable, London, 1914.

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MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER VII.

Mutations in Animals.

IN animals, the evidence for polymorphism arising through mutation is equally extensive, and a study of any group systematically reveals innumerable instances. As with plants, many of the forms arising in this way, especially in conditions of captivity where selection is eliminated, are to be classed as abnormal, but there are many others to which this does not apply. They represent innocuous or occasionally even advantageous changes, or changes which would be advantageous in certain environments.

One of the convincing cases of an expanding polymorphic group whose various types are mutational in origin is to be found in the land-snails. Gulick (1905) studied the Achatinellidæ of Hawaii, and the consideration of isolation as an evolutionary factor is frequently based on his work. More recently Crampton (1917) has investigated the related land-snail genus *Partula* of the Society Islands. It is well known that each valley often has its own peculiar species or varieties of snails, and this is the classical case of evolution under isolation. From the later studies it has become clear that isolation is not a *factor* of evolution but a *condition* in which evolution by mutation may take place.

Crampton's extensive study of the genus *Partula* in Tahiti has led to definite and well-subtantiated conclusions. Over 80,000 individuals were collected during visits in the years 1906 to 1909. Accurate records of the distribution of species and varieties had been made by Garrett in 1884, and it was thus possible to determine what changes in the snail fauna had taken place during the intervening 25 years. During this period a number of new forms have

arisen, evidently by mutations, and others have extended or in some cases retracted their area of distribution. The writer states that "mutation has been demonstrated in numerous instances, and in many species belonging to several islands." It is concluded that the morphological differences which appear are due to "spontaneous congenital causes that remain unknown in themselves" but whose effects are produced independently of environment, isolation of the forms in different valleys merely preventing an intermingling of populations.

To mention a few cases of variation in the Tahitian forms, *Partula otaheitana rubescens*, an exclusively sinistral sub-species, occurs in red and yellow varieties, the former being apparently a a simple Mendelian dominant. *P. o. affinis* has a dextral coil, but sporadic sinistral mutants occur. Similar reversals of symmetry are also known in other Gasteropods, such as *Crepidula*. In *affinis* the dimensional characters were found to vary from valley to valley. A banded form found by Garrett in a restricted locality now occurs in 20 separated regions of Tahiti, apparently as the result of independent mutations in the local populations. A red-banded form was also found by Crampton—an entirely new bicoloured pattern. Giants also appear in the sub-species *affinis* and *sinistrorsa*, and dwarfs in certain colonies of *rubescens* and other large snails. With regard to inheritance of banding in land-snails, Lang (1912, etc.) has interpreted it in Mendelian terms from breeding experiments with the European *Helix hortensis* and *H. nemoralis*.

In the plumage of birds, dichromatism or the existence of two interbreeding colour varieties, is a characteristic of many species, and the condition has apparently arisen through a mutation. As a typical case, the red and grey phases of the North American owl, *Otus asio*, have been discussed elsewhere,[1] the red being apparently a simple Mendelian dominant to the grey phase.

A remarkable case of an inherited variation in goats, which involves the nervous system, is recorded (Hooper, 1916) from Tennessee. In the central and eastern part of the State there is a breed in which, when suddenly frightened, the hind legs become stiff and the animal jumps along. If greatly frightened the front legs also become stiff and the animal falls to the ground rigid. These stiff-legged goats are preferred because they do not jump fences, but it is obvious that in nature such a variation in any mammal with preying enemies would be eliminated by natural

[1] Gates (1917c).

selection. It seems reasonable to suggest that the so-called death-feigning instinct in many insects probably originated in the same way. So far as I know, this is the first suggestion of a mutation in an instinct. It would be selected in those insects in which such action would save their lives.

The hornless condition in cattle is another mutation of much interest. Horns are known from the palæontological record to have undergone a gradual progressive development in various groups of Mammals, while in the polled breeds the horns have apparently been suddenly lost through a mutation. Punnett[1] has suggested that the hornless condition may have co-existed in a species along with the gradual development of horns. Since the polled condition is dominant, however, at least in cattle, the recessives would all be devoid of a factor for hornlessness. And since the horns are a highly serviceable and necessary weapon of defence in the wild species, it seems very probable that the original hornless type would be stamped out by selection as soon as horns developed far enough to become a valuable weapon. This would take place whatever the causes of the progressive development of horns. There are no traces of hornless cattle before the historic era, although Herodotus describes the domestic cattle of the Scythians as hornless. In the last two centuries many hornless varieties have arisen and the origin of some polled breeds is known.[2] The hornless mutation is in a sense a reversion as regards that character, and as such is comparable with peloria in flowers. The polled Hereford breed originated from a mutant at Atkinson, Kansas in 1889.[3] Being dominant, it cannot be supposed to have been present in the germplasm before its external appearance.

An interesting and little known work by Bonavia (1895), while containing some unacceptable ideas, devotes a chapter to monstrosities as probable factors in the creation of species. Among fishes are cited the sword-fish *Histophorus gladius* with its upper jaw prolonged, *Hemiramphius* and various others with the lower jaw prolonged; also *Zygœna* the hammer-headed shark, which may have originated monstrously by a projection of both ocular regions. A hairless condition is normal in certain races of Chinese and Mexican dogs. It occurs as an anomaly in horses cattle and dogs, and hairlessness in man "may have occurred all of a sudden

[1] Mendelism. MacMillan.

[2] See MacDonald and Sinclair, 1882. History of polled Angus cattle.

[3] Walter, H. E. Genetics, MacMillan, 1913.

as a monstrosity." Featherless birds are not unknown, or only certain pterylæ may be affected, as in the bareneck fowls (Davenport, 1914), a condition which is dominant in crosses. A well known case cited by Stebbing is that of *Dorippe dorsipes* with four legs, and four more small ones on its back. It is therefore clear that even mutational monstrosities have played their part in the production of species, and it is quite certain that if some family and ordinal characters could have been seen at their first appearance they would have been considered monstrosities.

Dwarfs and giants are as common in animal species as among plants. A dwarf-bearing strain of guinea pigs is described by Miss Sollas (1914). It produced in all 192 normals to 64 dwarfs, the latter evidently behaving as a simple Mendelian recessive. The study of inheritance of melanism in British Lepidoptera has in recent years attained considerable proportions. These results can only be touched upon here, but they show that the melanic variety usually behaves as a Mendelian dominant, sometimes a recessive, and in certain cases gives blending inheritance. A number of cases are discussed by Bateson (1913, p. 135 ff.)

Sumner (1917) has obtained mutations in the Californian deer-mouse, *Peromyscus maniculatus*, both in the wild state and in captivity. A "yellow" mutation of *P.m. gambeli* was trapped at LaJolla, California in 1914. The normals have a dark gray pelage and black eyes. In cages a total of 14 normal to 7 yellow appeared, in broods which were traced back to a single pair of grandparents. There were no other yellows among over 400 *gambeli* bred. Hence the appearance of the yellow was due to a recessive mutation factor carried in the two grandparents. Castle has reported similar "yellow sports" in wild species of *Microtus.*

CHAPTER VIII.

Limitations of the Cell Theory.[1]

The work of the present century in experimental breeding and cytology has led to many new points of view and new lines of approach to old problems. It therefore seems desirable to examine our present bearings from the point of view expressed in previous chapters. That the experimental method of attack upon the problems of variation and heredity, as well as those of embryology, is sound and of the utmost value cannot be gainsaid. On the other hand, it does not follow that the older conceptions of evolution, natural selection, and the inheritance of acquired characters are necessarily unsound or, if adhered to, subversive of the modern experimental results. We wish to show (1), that the experimentalist point of view resulting from the work in mutation and Mendelism is frankly antagonistic to the views of many palæontologists, anatomists and others who deal with the non-experimental data of evolution involving orthogenesis and the inheritance of acquired characters (2), that while these two factors bear entirely different relations to evolutionary changes, both are necessary to account for evolution as it has taken place.

It may be said that the divergence between the geneticist point of view and that of the biologist who relies upon the historical background of evolution for his interpretation of evolutionary factors has long been manifest; and that is true. Yet we venture to think that no one has clearly visualized or set forth the fundamental character of this antagonism in relation to the structure of the organism. Moreover, those who have recognised the opposition between the principles of germinal variation and inheritance of acquired characters in evolution have usually endeavoured to solve the difficulty by denying or ignoring one principal and affirming the other. Rather, we think it necessary to harmonize these two conflicting views into a more complete and balanced conception of the evolutionary process.

We propose, then, to show that higher organisms exhibit two sharply contrasted types of characters which differ fundamentally, (1) in their manner of origin, (2) in their relation to the structure of the the organism, (3) in their relations to such phenomena

[1] The following chapters are chiefly based on a discussion "On the Existence of two fundamentally different types of characters in Organisms," which took place at the Linnean Society, February 5th, 1920.

as recapitulation, adaptation, inheritance, and distribution. The first class of characters are (as already expressed in Chapter II.) cell-characters, which have arisen through mutations, are represented in every cell of the organism, and are usually inherited as distinct units. Since they arise in and are carried by the nuclei they may be called *karyogenetic.* To the second category belong characters which arise gradually in the organism through impact of the environment or through "orthogenesis,"[1] may apply only to localized portions in the life-cycle of the organism, and at first are not incorporated in the germplasm. Such characters we may call organismal[2], in contradistinction to cell-characters. Organismal characters may imply an increase in the length of the life-cycle, as strikingly evidenced in so many animal larvæ which undergo metamorphosis, or they may show stages in shortening, as in the gametophytes of many higher plants.

The attitude of experimental biologists to the questions of recapitulation and inheritance of acquired characters (although the former has never fallen into the same disrepute as the latter) has been generally one of skepticism and denial. Reasons for adopting a different position may be given as follows: (1) the difficulty of explaining adequately the abundant facts of recapitulation in plants and animals by means of mutations or changes originally germinal; (2) the logical necessity of the principle of functional inheritance in some form to explain the origin of embryonic recapitulatory characters involving adaptation; (3) the approach to an understanding, through such agencies as hormones and enzymes, of how the transmission and ultimate germinal fixation of somatic modifications may take place; (4) the slowly accumulating direct experimental evidence for parallel induction and the transmission of modifications.

In contrasting organismal with cell characters we are contrasting two points of view regarding the organism which are at least as old as Aristotle and Empedocles. Modern representatives of these views speak of the organism as a whole on the one hand, and of elementalist or particulate theories on the other. It scarcely needs pointing out that elementalist conceptions, particularly of

[1] An orthogenetic result may also of course arise from a succession of germinal changes or mutations following each other in any line of phylogeny.

[2] In the Linnean discussion, Professor F. E. Weiss suggested the obvious antonym *cytogenetic* for this category of characters, since they are apparently cytoplasmic in origin. This term had already been considered, but was finally discarded because "organismal" expressed better the idea desired. Never theless it will be a useful term in certain connections.

heredity and variation, have had a wide vogue in recent years. On the other hand, Loeb (1916) and from a different point of view, Ritter (1919), among others, have recently championed the organism-as-a-whole. The latter writer has pressed this view farthest, in the endeavour to eliminate elementalist conceptions altogether. We believe a truer attitude lies in the recognition of a fundamental truth in both these aspects.

In a former work[1] and in earlier chapters of this series we developed a cell theory of mutations emphasizing the fact that each new form arises as a germinal *difference* from the parent type. The cell unit, in all such variations, is the thing which has changed, and the new external characters which appear in every part of the organism are the structural result of an ontogeny built up with a different unit as basis.[2] This situation was particularly clear in *Œnothera gigas*, where it was shown[3] that the volume of the nuclei and cells has increased in varying proportions in different tissues. Tupper and Bartlett (1916) have confirmed and extended these results in the case of *Œ. stenomeres* mut. *gigas* which is also tetraploid or $4x$ in the constitution of its nuclei.

Without going farther afield for confirmatory data, which are amply furnished in the contemporary literature, we may conclude that the mutation theory of germinal variations is firmly grounded upon the cell theory, and if the cell theory were universal in its application then mutations or germinal changes might be supposed to supply the whole of the material for evolution in organisms. Facts such as those pointed out above lead to the concept of the species cell. This is a conception which has been independently arrived at by different lines of approach (see, for example, Lang, 1909). It is a sounder and less extreme conception than that of the organism as a cell-state, *i.e.*, merely an aggregation of more or less independent cell units.

Biologists have long recognized the necessity for limitations of the cell theory of organic structure. On the one hand we have the legitimate and necessary conception of the species cell, briefly set

[1] The Mutation Factor in Evolution.

[2] If this be the case, then the mitoses during ontogeny do not bring about the unequal division and sorting out of portions of the chromosomes, as Weismann supposed; but all these divisions are, as they appear, equational so far as the chromosomes are concerned. This conclusion has also been reached from the study of experimental embryology (Conklin, 1916) and from other lines of approach. So far as the chromosomes are concerned, their materials are apparently not as a rule segregated by differential divisions during ontogeny. On the other hand, differential divisions of the cytoplasm are of frequent occurrence.

[3] Gates, 1909a.

forth above, implying that germinal changes arise in a fixed life-cycle through a change in the cell unit which is represented in every nucleus and therefore may modify every stage of the new organism.[1] On the other hand, if the more fundamental facts of recapitulation mean anything, they imply that at some time an actual lengthening of the life-cycle has taken place, either by the addition of cell divisions at its end or by their intercalation at some point. Such a process can not easily be accomplished by a variation in the structure of the cell or nuclear unit itself, but must rather be the result of the organism as it were overcoming its cell shackles and by its own energy producing new developments, though such novel additions are themselves cellular in structure.

From the time the foundations of the cell theory were laid by Schleiden and Schwann in 1838-39, its universal sway was scarcely questioned for over half a century. During this period it was established that cells arise only from the division of previous cells, and the cell theory culminated in such conceptions as the physiological division of labour among cells, the mosaic theory of embryonic development, the individual as the sum of the activities of its various cells. In short, it came to be assumed that cells make the organism, while the contrary fact that the organism after all makes its cells was tacitly or explicitly denied. In the same way it was assumed that each cell of a multicellular organism necessarily corresponded with the whole organism in the Protozoa.

One of the first reactions from this extreme development of the cell theory, which made the organism not a master in its own house but a slave of its constituent cells, was a well known paper by Sedgwick (1894) on the inadequacy of the cell theory of development. His views were based on studies of the embryos of *Peripatus capensis*, which he believed were essentially cœnocytic in structure; also upon the development of mesenchyme and nervous tissue in Elasmobranch embryos. As far as Peripatus is concerned, delicate cell walls have recently been demonstrated (Glen, 1918) both in the ectoderm and endoderm layers, by careful preparations and the use of an immersion lens. But their demonstration does not affect the fundamental question of the relation of the cell to the organism, for, to mention only a few cases, it is well known that in the formation of the blastoderm of the insect egg, as well as in the early stages of development of the female gametophyte and proembryo in Gymnosperms, a stage is passed through in which

[1] It appears that, especially in animals, the change is frequently visible or obvious only in certain organs.

there is multiplication of free nuclei,[1] which arrange themselves in a particular manner, but without the formation of cell walls until later. That cells can develope within a cell is also well exemplified in the development of the embryo-sac of Angiosperms.

In the same year Whitman (1894), in a notable paper, attacked the cell theory on fundamental theoretical grounds. He concluded that the formation of the embryo is not controlled by the form of the cleavage. "The plastic forces heed no cell-boundaries, but mould the germ-mass regardless of the way it is cut up into cells." His position was that "organization precedes cell-formation and regulates it."

It is impossible here to enter into a discussion of the various views which grew out of the extensive studies on cell-lineage, but granting the accuracy of the above limitations of the cell theory, it will be seen that they are in no way out of harmony with the view of mutations as cell variations, or rather nuclear variations, previously expressed. Another limitation of the cell theory will be considered in the next chapter.

[1] Incidentally it may be pointed out that any comprehensive theory of heredity must be one which is applicable equally to those cases in which regular cleavage of the egg takes place and those in which in one stage the embryo contains free nuclei. Since the nuclei are the only structures in common, and the laws of inheritance remain the same in both cases, *ergo* the nuclei and not the planes of cleavage must determine those laws.

CHAPTER IX.

The Recapitulation Theory.

The recapitulation theory has had many vicissitudes both in its application to plants and to animals. The conception has been stated and restated many times in varying terms, but that ontogenetic stages may have a phylogenetic significance has rarely been denied and has more often been implicitly assumed. The principle was tacitly recognized even before Darwin, and he accepted it practically without reserve. Indeed it was one of the foundation stones in his argument for evolution.

It is desirable also to point out that any theory of recapitulation which is to have any significance in the interpretation of life histories must recognize that in the last analysis recapitulation implies that at some stage in the evolution of any group an increase in the life-cycle took place, by the addition of certain stages. This is in sharp contrast with a germinal change, which necessarily modifies every stage, at least internally as regards nuclear structure, but can hardly be held to add anything to the adult stage of development, or in other words to increase the number of stages in the life-cycle.

Recapitulation and the alternation of generations in plants.

As regards plants, it may first be pointed out that the theory of the antithetic alternation of generations, which has been widely adhered to by botanists and has been given its most notable expression in the classic volume of Bower (1908) on *The Origin of a Land Flora,* implies from the evolutionary point of view a continued lengthening and increase in complexity on the part of the sporophyte, and in seed plants a contemporaneous shortening and simplification of the gametophyte. This theory runs like a golden thread through all the speculations concerning the origin and larger relationships of the main groups of vascular plants, and there is nothing quite corresponding to it among animals. In the able hands of Bower, it implies that the sporophyte generation resulting from the fertilized egg is intercalated between two gametophyte generations and has gradually increased in complexity or length through the Bryophytes, Pteridophytes, Gymnosperms and Angiosperms in connection with their gradual transition and adaptation from aquatic or moist to typically terrestrial conditions.

True, the theory of homologous alternation in plants has also been held, though not so widely. It was for a time based chiefly

on the facts of apogamy and apospory in Ferns, and experimentally induced apospory in Bryophytes (Lang, 1901). But even when of natural occurrence, these are generally admitted to be exceptional conditions of recent development. The careful cytological studies of apogamy and apospory, however, led Farmer and Digby (1907) to the conclusion that these phenomena leave the question of alternation essentially where it was. It need only be pointed out here that the theory of homologous alternation of generations in plants corresponds to such a view as would restrict the significance of recapitulation to a great degree; while an important phase of the antithetic theory is that it implies a *lengthening* of the sporophyte generation in connection with the adaptation of plants to a terrestrial habitat.

In his original studies of apogamy and apospory, Lang (1898) carefully refrained from giving his views a bias in either direction. More recently (Lang, 1909) he has propounded an interesting conception of homologous alternation from an ontogenetic point of view.[1] Briefly the view begins with the concept of the species cell, based on the fact that any cell of the species is potentially able to reproduce the whole plant. This being the case, "the haploid and diploid germ-cells have potentially the same morphological properties." But they are believed to develop different generations because the germ cell is exposed to different conditions in initiating the two generations. This interesting suggestion, however, encounters many serious difficulties, some of which were pointed out in a criticism by V. H. Blackman (1909).

It cannot be said that the homologous view has received wide support as regards Archegoniates and their descendants, but on the other hand important evidence has developed for the occurrence of homologous alternation in Algæ. It is significant that in this group the gametophyte and sporophyte generations develop under the same relatively uniform conditions, exposed to sea water, and they are morphologically alike. Without discussing the subject in any detail,[2] it may be pointed out that Yamanouchi (1906) found in the red alga Polysiphonia an alternation of generations, which he regarded as antithetic, between tetrasporic plants having 40 chromosomes and sexual plants with 20, the cystocarp being a part of the sporophytic phase. Lewis (1909), in a study of another of the Rhodophyceæ, Griffithsia, has taken up a more advanced position

[1] See also the discussion on alternation of generations at the Linnean Society, published in New Phytol. 8: 104-116, 1909.

[2] For recent discussions of the life-cycles in Algæ see Fritsch (1916) and Davis (1916).

which appears to be well justified by the facts. The life history of Griffithsia is in general parallel to that of Polysiphonia, the tetrasporic plants apparently having 14 chromosomes and sexual plants 7, though there is some doubt about the accuracy of these counts.

According to the views of Lewis, there is (1) an antithetic alternation between sexual plants, representing the gametophytes, and the sporogenous cells of the cystocarp, representing the sporophyte, (2) a regular succession of tetrasporic and sexual individuals representing an homologous alternation of generations but not equivalent to the alternation in Archegoniates. He believes that the tetrasporic plant has been intercalated in the life history, not through the "gradual differentiation of a simple product of the germination of the zygote," which is the pith of the antithetic theory; but, as Yamanouchi suggested, through the suppression of chromosome reduction in the formation of a carpospore which then at once grew into a tetrasporic plant.

In concluding a brief survey of this very large subject of alternation, we may remark that the antithetic theory, which continues to receive the larger number of adherents, implies just such a lengthening of the life-cycle as is indicated by recapitulatory phenomena. The homologous theory, on the other hand, would account for the alternation through the sudden intercalation of a generation in Algæ as the result of a change in spore development which is essentially mutational. In Archegoniates, the homologous view would apparently imply the gradual simultaneous progressive differentiation of gametophyte and sporophyte through differences in the environment in which the asexual spore and the fertilized egg develop. But as Farmer[1] has pointed out, it is impossible to imagine how the Bryophyte sporogonium at any rate could have arisen through modification of the gametophyte. It seems clear that this structure at least must represent an intercalated phase progressively developed. Each group of plants must then, as Farmer has emphasized, be separately considered on its own merits, on the basis of the historical probabilities as determined by comparative morphology.

Recapitulation phenomena in Gametophytes.

It may be noted in passing that although plants "climbed out of the water" at a remote period, yet large groups of Bryophytes and Pteridophytes still survive although imperfectly adapted to life on dry land. This, as Bower points out, is probably because the

[1] New Phytol. 8: 113, 1909.

sporophyte has developed far enough to make possible the production of spores in sufficiently large numbers to ensure the passage through the difficult stage in the life-cycle when water is a necessity for the accomplishment of fertilization. Only in vascular plants above the Cycads has complete adaptation to terrestrial conditions been accomplished, by the adoption of siphonogamy and the loss of swimming sperms.[1] Nevertheless, the higher siphonogamous plants do not, except in rare instances, show recapitulation stages of their gametophytes. In other words, the gametophyte development is usually direct. This can hardly be because the gametophyte in its later evolution forms a reduction series, because among animals the most remarkable and convincing instances of recapitulation occur where degeneration has taken place as a result of parasitism or the adoption of sedentary habits. Typical recapitulation phenomena do nevertheless appear in plant gametophytes. For instance the archegonium, which is so characteristic an organ in Bryophytes, and has given an aggregate name to the three great groups in which it occurs, persists in a progressively reduced form throughout the Gymnosperms until we reach the higher Gnetales, although in certain Araucarians (Eames, 1913) it has become a positive hindrance to fertilization. In this case the archegonium neck cells have developed into a thick-walled structure which the pollen tube cannot penetrate. But the jacket-cells adjacent to the neck are actually eliminated, thus making it easier for the pollen tube to reach the central cell. No more striking case could be cited of the continued production of an organ which not only has lost its function but which is a positive hindrance to the functioning pollen tube, though its retention has entailed other structural changes in the jacket-cells to facilitate fertilization.

Thus throughout the Gymnosperms, the gametophyte is being reduced, and recapitulation phenomena which suggest an ebbing tide occur in its terminal stages. The archegonium itself shows a gradual series of reduction stages until it is finally eliminated. In the lower Gymnosperms it has already lost the neck canal cells found in the archegonium of Mosses and Ferns, and among the Conifers the ventral canal cell is gradually eliminated. In the Abietineæ (see Coulter and Chamberlain, 1910) a ventral canal cell is cut off, in the Araucarians the nuclear division takes place but no cell wall is formed ; or in some species of Pinus a wall may be

[1] It is well known that similar types of adaptation from aquatic to terrestrial conditions have occurred in the Fungi, involving the loss of free swimming gametes and the development of some form of siphonogamy.

formed in some instances and only a nucleus in others. In every case this ventral canal cell or nucleus is only a reminiscence which continues to reappear as a terminal stage although in its origin it dates back at least to the Liverworts. But it appears to be finally eliminated in the Taxodineæ. The cases just cited, however, do not involve recapitulation so far as the individual ontogeny is concerned. They are only seen to be closely related to such phenomena from a comparative phylogenetic point of view.

Such a reduction series Coulter (1915) no doubt justly considers to represent the expression of an orthogenetic tendency, though whether it is the result of climatic differentiation is not so clear. The series derives its interest from the fact that the higher Gymnosperms, in which the archegonium is quite eliminated, must have had ancestors in which that reduction gradually took place. From our present point of view, the explanation cannot be found in a series of successive nuclear variations or mutations, for these would make themselves felt in other parts of the organism, affecting many characters in a correlated fashion. Though the argument is by no means conclusive as regards this matter, yet it seems most reasonable to consider these as organismal characters and to explain the shortening of the gametophyte generation in the same way that recapitulatory characters find their explanation. The direction in which that explanation is to be sought will be discussed below.

Another support for this view may be found in the fact that the chromosome number is remarkably uniform throughout the Gymnosperms, being, with few exceptions, 24. If the evolution of the Gymnosperms had taken place largely through mutations, *i.e.*, through changes arising in the germinal chromatin, one would expect it to have produced some effect on the chromatin morphology in the various species. The Angiosperms, by contrast, in which there is evidence that much mutation has taken place and is now going on, are characterized by remarkable variety in number, size and shape of their chromosomes even within single families or genera. The same is true of insects.

Other cases of ancestral reminiscence in gametophytes, as though the organism repeated certain stages from force of habit or from some source of energy impelling its development forward, are to be found in Angiosperms. In the nuclear divisions within the embryo sac an evanescent cell-plate sometimes appears on the spindle. But this reminiscence of wall-formation soon disappears along with the spindles. The same is true of the prothallial cells

in the male gametophyte of many Gymnosperms. There is one such cell in Cycads, which persists. Ginkgo has one ephemeral and one persistent prothallial cell which are cut off in succession by the side of the microspore, while in Pinus both prothallial cells dwindle promptly to small dark-staining masses, as though the life had quickly gone out of them. The nucleus may begin to disorganize even before the cell-plate is formed. Such structures represent momentary stages of an ebbing tide. In *Picea canadensis*, Hutchinson (1915) has found all these and other conditions to occur as variations.

Recapitulation in the Sporophyte.

If now we turn to the sporophyte, we find again many of the most striking cases of recapitulation in Gymnosperms. Indeed they appear to be of more frequent occurrence in this group than in any other plants. A possible reason for this has already been suggested, namely the relative infrequency of mutations. It is well to keep in mind also that recapitulation in the sporophyte usually indicates adaptation to altered conditions. Among well known instances in Conifers may be cited the genus Phyllocladus, characterized by an absence of leaves, the branches forming flattened leaf-like expansions. The seedlings, however, have a terete axis bearing ordinary leaves and this obviously represents the ancestral condition, from which for some unknown reason the genus departed. That such an alteration is not mutational is indicated, according to the present interpretation, by the fact that the ancestral condition is thus clearly present in the earlier stages of ontogeny. A mutational change, being represented in every nucleus from the fertilized egg onwards would have eliminated, or rather transformed, this juvenile stage. In Œnothera, as de Vries (1909) pointed out, the first leaves after the cotyledons make it possible to recognize a mutant form.

To mention three other cases of recapitulation in Gymnosperms: A feature of the genus Pinus is the occurrence of dwarf shoots, each bearing a fascicle of needle leaves. But in the seedling the leaves are scattered on the stem as in other conifers. Similarly the genus Larix, unlike most conifers, has deciduous leaves; but in the juvenile stage the leaves adhere for several years. In the Mariposa grove near the Yosemite valley in California I observed that *Sequoia gigantea* is a number of years old and many feet high before its foliage acquires the characteristic appressed form. When grown in the English climate, this appressed type of foliage appears never to be quite reached even in old trees.

Other writers have carried the principle of recapitulation much farther, and notably Jeffrey (1917), who applies it to the histological structures of vascular tissues, and further finds that regeneration after wounding frequently leads to the reappearance of ancestral characters. This principle is freely used by him in the comparison of living with fossil forms, and in the interpretation of phylogenies. To cite examples from the Araucarian conifers, it has long been known (Thistleton-Dyer 1901) that in the adult stem of these trees, owing to the continued activity of a cambium the leaf traces have the peculiarity of being persistent for many years after the leaves have fallen. Another well known peculiarity of Araucarian wood is that the bordered pits in the xylem tracheids are alternate in origin, not opposite as in other living conifers. Jeffrey (l.c., p. 236) points out that in Mesozoic araucarian woods belonging to the genus Brachyoxylon the leaf traces persist only for a short time, and the bordered pits are not alternating and crowded as in the living genera. In seedlings of the modern Agathis and Araucaria, however, " the leaf trace persists only so long as it is related to a functional leaf," and the pitting is like that found in the Cretaceous Brachyoxylon. Such a striking case of recapitulation—and others of like nature are known—can hardly find its explanation in a germinal change which belongs equally to every cell.

While these principles of recapitulation seem for the most part well established, caution must of course be used in their application, especially in these more complicated cases; for it would be easy to deduce incorrect phylogenetic conclusions by attaching more significance to such cases than they really possess. It is important also not to lose sight of the fact that recapitulation phenomena occur where there has been adaptation to new conditions. Such changes are often climatic, but may also be environmental in the widest sense.

One instance of more doubtful recapitulatory phenomena in plants must suffice. In a recent paper on Rhododendron seedlings, Professor Balfour (1917) has shown that many of the species in their earlier years pass through a series of changes in the pigmentation and pubescence of their leaves. Thus in *R. adenogynum* Diels the under surface of the leaves is red glandular in the seedling. But about the third year the redness disappears as well as the glandular hairs. After some seven years the buff-coloured tomentum of long, interwoven, branched hairs begins to show at the base of the (now green) leaves, and gradually in later years

covers the whole under surface of the leaf. Similar developmental changes take place in a number of other species.

Balfour thinks this developmental modification is in relation not to a climatic change in the habitat of the species, but to the differences in environmental conditions as regards, light, moisture, heat and air currents encountered by the leaves of the young plant near the soil and of the older plant at a higher level. He points out that a higher temperature and a more rapid metabolism (subserved by anthocyanin) are important at first, while control of transpiration (subserved by tomentum) is important later.

The above case could not be regarded in itself as evidence of recapitulation, but it serves to show how indubitable recapitulatory phenomena shade into those which have only a physiological or ecological rather than an ancestral significance.

Summarizing the data of recapitulation in plants, we may say that recapitulatory characters are found chiefly (1) in the seedlings of Gymnosperms and some Angiosperms, (2) in the terminal stages of gametophytes, (3) in wood structure; but as a rule they have been lost from the ontogeny through the cellular development becoming direct. If the antithetic theory of alternation of generations be correct, however, then a large part of evolution has been concerned with the gradual development of characters which were originally organismal and have become in some measure recapitulatory.

Recapitulation in Animals.

Important and significant as are the indubitable cases of recapitulation in plants, the phenomenon is much more prevalent in animal development. This may perhaps be connected with the fact that the animal in development may be said to have greater power over its cells owing to their thinner walls and greater plasticity.[1] A striking phenomenon in the cleavage of animal eggs is the mutual readjustment of the cells with relation to each other which goes on after each cleavage.[2] In this way the forces of the

[1] A number of facts indicate that in some respects animals have greater powers of regulation than plants. One need only mention (*a*) phenomena of metamorphosis in which tissues may break down and be used again in the building up of new structures; and (*b*) the fact that in Metapodius (Wilson 1910) and Drosophila (Bridges 1916) the presence of one or even several extra chromosomes (duplicates of one member) in the nuclei produces no external alteration; while the duplication of one chromosome in Œnothera produces striking external differences. The recent studies of Rosenberg (1918) on Crepis indicate that here also the duplication of a pair of chromosomes alters the external features of the plant.

[2] It is a well known fact that cleavage itself is a rhythmic process, in which a period of simultaneous nuclear division alternates with a period of nuclear growth, and this rhythmic alternation is accompanied by a physiological rhythm in CO_2 production, permeability, etc.

organism can, as it were assert a power over the cells in maintaining a unity of structure during development to a degree which is not possible with the thicker cellulose walls of plants, though in woody stems growth-pressure produces a certain amount of such readjustment of dead cells. In any case, whatever the reason, it remains true that while development in plants is usually direct, and recapitulation the exception, the animal embryologist is confronted with recapitulation on all hands with such amazing profusion that a comprehensive principle is more obviously required for their explanation.

Another explanation of the difference between plants and animals in the occurrence of recapitulation may lie in a greater frequency of mutations in the phylogeny of plants. Also, animal groups in their evolution have probably passed more frequently by adaptation from one habitat to another. Witness, for example, the number of groups from Ephemeridæ to whales or penguins which have become secondarily modified for an aquatic life. Even when a like occurrence happens in plants, the stages of it are often nearly or quite obliterated by short-circuiting. It is therefore quite unsafe to argue in the case of plants that because a given adaptational character shows no recapitulation in development it must have originated through a germinal change. Such an attitude stands a better chance of being sound in the case of animals.

Concerning the facts of recapitulation, MacBride's textbook of embryology—Invertebrata (1914) is a veritable mine of information. His attitude represents a return to an interpretation of the significance of larval stages in relation to phylogeny on a frankly neo-Lamarckian basis. Embryologists of the last two decades have largely endeavoured to avoid this attitude, but without conspicuous success. MacBride assumes that larval stages represent actual ancestral groups of organisms. It is also significant, as we pointed out in the case of plants, that the recapitulation seems always to have originated in connection with the adaptation of the animal to a new set of conditions.

Although we have never seen it explicitly stated that embryonic recapitulation implies the inheritance of acquired characters,[1] yet it is probably the tacit recognition of this fact which has led to the denial of recapitulation by those who believe only in germinal variations as material for evolution.

[1] Since this was written I have received from Professor MacBride (1917) a paper which I had not previously seen, in which it is definitely stated that recapitulation implies the inheritance of acquired characters, and citing a number of cases in support of this view.

Zoologists are generally agreed that the nauplius and zoæa larvæ of Crustaceans and the veliger larva of Molluscs represent ancestral stages; similarly, that the trochophore larva of Annelids and Molluscs shows these two very divergent groups to have been derived from a common ancestor. MacBride would go further and say that the trochophore is a smaller and somewhat reduced or specialized representative of that ancestor. According to the interpretation here adopted, the various larvæ at one time represented *terminal stages* in their respective life-cycles, and by subsequent evolution they were not modified out of existence or out of recognition through germinal changes, but became subterminal through the *addition* of later stages to complete the ontogeny. In a field where every larva has its ancestral significance, it is almost invideous to single out particular cases for illustration. The tadpole of Ascidians, which gave the first hint of the Chordate affinities of this group, is a striking instance. Only the degeneration and special adaptations resulting from the adoption of a sedentary life can account for their remarkable transformation, and we fail to see how it can be adequately explained except on a neo-Lamarckian basis. An equally irrefutable case of recapitulation is that of the feather-star Antedon, whose egg developes into a free-swimming larva which later becomes fixed by a stalk. This fixed stage corresponds with the modern genus Pentacrinus. The adult feather-star developes cirri and, losing its stalk, becomes free again. Can anyone pretend to believe that this remarkable series of transformations does not recapitulate the history of the race? And, if so, how can one avoid the conclusion that the life-cycle has been lengthened?

A type of recapitulatory character corresponding to the appearance of evanescent stages in the gametophytes of the Gymnosperms, is found in certain nauplius larvæ. MacBride (l.c. p. 204) regards the nauplius as representing the common ancestor of all Crustacea. He says, "When the larva does not hatch out as a nauplius, a cuticle is produced and shed by the embryo whilst still within the egg shell when it reaches the nauplius stage, thereby showing that formerly this stage must have been passed through in the open, in the ancestors of the forms in which it is now purely embryonic." Again, in the oyster, which has no foot and becomes permanently attached by one valve of its shell, the veliger larva nevertheless possesses a functional foot which is therefore a recapitulatory character.

Perhaps the most convincing of all cases for a Lamarckian interpretation of recapitulation is that of the parasitic Copepod, *Achtheres amblopltitis*, where as MacBride remarks, "we may almost say that the ancestor is known." The adult is a parasite on the gills of the rock-bass, and is a sac-like organism devoid of all semblance of Copepod structure, yet the animal passes through a brief larval stage which anyone would recognize at once as representing a typical Copepodan genus. Whatever explanation applies to this remarkably clear case must also apply *mutatis mutandis* to the whole series of larval stages which represent the remoter ancestry in other organisms. We think this case furnishes one of the clearest evidences of the sharp contrast we are endeavouring to draw between recapitulatory and mutational, or in other words, between organismal and karyogenetic characters. Yet it is admitted that even in this Copepodid larva there are modifications from the typical details of Copepod structure. But they follow the usual lines of diminution in size of the larva and consequent reduction in the number of metameric parts. Another factor which tends to obscure ancestral stages is the well-known principle of telescoping, or the earlier appearance of embryonic organs, which has been called heterochrony by Lankester, or tachygenesis by French writers (Perrier and Gravier, 1902). That embryonic and larval stages can also undergo special modifications of an adaptational nature is another well recognized principle which tends to obscure ancestral relationships.

Many of the battles of recapitulation have been fought over the frog, so we may briefly examine his case. Some embryologists have gone so far as to deny any ancestral significance to the tadpole. While the other extreme view, that all larval characters of the frog have ancestral significance, is certainly disproved; yet the truth evidently lies in a recognition of the fact that in the tadpole as in most other larvæ, there are some recapitulatory or palingenetic characters and some adaptational or cœnogenetic characters. The obvious recapitulatory characters are the fish-like tail, gill arches and blood system. It seems impossible to avoid the conclusion that these were once terminal developmental stages, in the frog's fish-ancestor. On the other hand Boulenger (1918) has pointed out that tadpoles have had an evolutionary history of their own and have developed special adaptational features. He enumerates (Boulenger 1897) "The horny beak and circular lip with its horny armature, the spiraculum, the enclosure of the fore-

limbs in diverticula of the branchial chambers, and such special adaptations as the ventral disc or sucker of certain mountain forms." The existence of such adaptational characters is supported by the fact that certain species differ more widely in their tadpoles than in their adult stages. Thus (Boulenger and Annandale, 1918) the Indian species *Rana tigrina* and *R. cancrivora* are so similar as frogs that the latter was classed as a variety of the former. But Annandale (l.c.) has shown that the tadpoles differ markedly in buccal armature. Whether this is a case of convergence of the adult species, as Dr. Annandale thinks, or divergence of the tadpoles, as Dr. Boulenger believes, need not concern us here, though from analogy the latter interpretation appears more probable.

To return to the recapitulatory characters, the transformation of the fish-like gill-arches of the tadpole into the aortic arches of higher vertebrates is too well known to require comment here, except to point out that it comes about through the gradual substitution of one series of blood vessels for another, the branches to the gills being gradually pinched off and the blood stream diverted to the more direct route to the lungs. The specious argument that the development of any recapitulatory character *must* go through such preliminary stages for purely structural developmental reasons is now seldom heard and can very well be consigned to oblivion. Developmental mechanics as well as comparative embryology tell strongly against it.

The experiments of Gudernatsch (1914) in greatly retarding or hastening the time of metamorphosis by feeding tadpoles on thymus or thyroid respectively, showing that growth and differentiation are separate factors, do not affect our present interpretation. They merely indicate that the processes of development and metamorphosis are physiologically controlled by something in the body of the nature of hormones or enzymes secreted by certain tissues. A recent paper (Morse, 1918) has attempted a further analysis of the processes that lead to atrophy of the tail in metamorphosis. The writer concludes that autolysis is the primary physiological factor. The first step in atrophy, according to Barfurth, is the growth of the pygostyle which, by occlusion of the blood vessels in the tail, causes an accumulation of CO_2 and acids. This acidosis of the tissues induces autolysis. In this condition the phagocytes are chemotactically attracted to the atrophying organs, so that phagocytosis is a secondary, and not the primary factor as Metschnikoff supposed. Hormones or enzymes probably stimulate

the development of the pygostyle, but something must in turn determine the development of these. Morse concluded from his experiments that it is possible to suppress metamorphosis, but that it cannot be induced in stages *far* removed from those in which it would normally occur. A certain cycle of events determined by heredity is necessary before any stimulating agent will cause metamorphosis.

Although we have spoken of recapitulatory characters having been at one time terminal stages in the life-cycle, yet it appears that they have not always been added terminally but have often been intercalated at a subterminal or earlier stage. Thus in plants the sporophyte ends inevitably with sporogenesis, so that the lengthening of the sporophyte generation must always have taken place through the addition of subterminal stages, involving the delay of sporogenesis.[1] In animals, too, spermatogenesis or oogenesis is usually delayed until the ontogeny is complete, although the greater freedom of the germ cells in their relation to the soma makes possible the occasional occurence of pædogenesis or reproduction by larvæ.

In concluding this chapter it may be pointed out that the phenomena of recapitulation furnish another limitation of the cell theory, recapitulatory characters being organismal, and embryonic recapitulation apparently involving the inheritance of functional modifications.

[1] This is a little different from Bower's well-known view of the sterilization of potentially sporogenous tissue.

CHAPTER X.

Inheritance of acquired Characters.

In the last chapter it was pointed out that adaptational recapitulatory characters have apparently not originated directly through chromatin variations, but indirectly *via* the cytoplasm. Under the influence of Weismann's conception of continuity of the germplasm, the very possibility of acquired characters or impressed modifications being inherited, was denied. Like so many other useful biological conceptions this was pushed to an extreme, and a non-existent degree of isolation and insulation of the germ cells from the soma was freely assumed. But in the last decade there has been an increasing tendency to adopt a more reasonable attitude to these problems. Weismann's conception of blastogenic and somatogenic variations or characters has also tended to lay too great emphasis on a distinction which can scarcely be said to exist at all in plants, except in sporogenesis, namely the segregation between germ cells and somatic cells. The contrast we have ventured to draw between karyogenic or nuclear characters and organismal or recapitulatory characters, seems more in accord with our present knowledge of the development, cytological structure and genetic behaviour of organisms.

In the meantime, experimental evidence for the inheritance of acquired characters and related phenomena has been slowly accumulating, but space will permit of reference to only a few papers. We may first mention Agar's (1913) work on parallel induction in the Daphnid, *Simocephalus vetulus*, where references to the related literature will be found. Agar discovered that when Simocephalus is fed on a culture of Protophyta the valves of the carapace became reflexed, the degree of this abnormality gradually increasing during successive instars or moults. If such individuals were removed to normal conditions before their (parthenogenetic) eggs were laid, these eggs nevertheless developed into adults showing the same abnormality which their parents had acquired ontogenetically through environmental impress. But the effect soon wore off in later generations grown in normal conditions.

Similarly, grown at higher temperature the animals were very much smaller, developed more rapidly and produced smaller broods. Eggs laid shortly after removal to ordinary temperature developed into adults nearly as small as their parents, but in F_2 little of the effect remained.

The parallel induction in germ and soma is believed to be brought about by "altering the nature of the metabolic products included in the living protoplasm." That such effects are transmitted for one or two generations is an excellent example of a cytoplasmic effect temporarily inherited, and indicates that minimal quantities of such substances are multiplied so as to produce a powerful effect. Kammerer claims to have obtained such a result in experiments with a lizard, where the character white instead of red belly, impressed by high temperature, was transmitted through the *sperm* to the next generation of adults.

The experiments of Kammerer (1909, 1919) with *Alytes obstetricans* have been much discussed. His recent results are largely confirmatory of earlier papers published ten years ago, and a number of other contributions, including an elaborate series of experiments with salamanders, have appeared in the intervening years. It is well-known that Alytes differs from other European Anura in that its strings of eggs are not laid in the water,[1] but are twisted round the legs of the male and carried for some time during their stages of embryonic development. Their bearer only resorts to the water when they are ready to hatch as advanced tadpoles having a single pair of gills covered by an operculum.

When these animals are kept at a higher temperature (25°—30° C.) with access to water, the eggs are laid in the water, and they hatch earlier, when the gills are still exposed. If these conditions are continued, so that the animals are obliged to breed in the water, by the F_4 generation the tadpoles will have three pairs of gills as in other frogs. A number of other interesting changes occur. The eggs of Alytes are much larger and less numerous than in other frogs and toads. Thus, *Rana* produces 600-4,000 eggs with a diameter of only 1·7 mm, while in Alytes the number of eggs is about 60 and they are 3·5-4 mm. in diameter owing to a great amount of yolk. Developing in the water, the eggs of Alytes become rapidly smaller in successive generations.

But perhaps the most critical of these results concerns the secondary sexual characters of the male. Here again Alytes differs from other Anura in the absence of the characteristic horny pad which developes on the thumb or wrist of the male during the breeding season, enabling him to retain his hold on the female while in the water. When pairing and egg-laying occur in the water, however, according to Kammerer this pad gradually appears in Alytes, until

[1] It is an interesting fact that in one locality, Münster in Westphalia (Kammerer, 1909, p. 452), the eggs are normally laid in water.

by the F_5 generation it is fully developed. This is said to be accompanied by an increase in the musculature of the arms. The development and regeneration of the pad are found to be independent of hormones from the sex organs, since castration of the males does not affect it. Also it is said that when F_2 males in which the patch had partly developed were crossed with normal Alytes females without a patch, a Mendelian result was obtained. This will certainly require additional evidence before it can be accepted.

The fact that in all Anura this pad only becomes apparent during the breeding season, seems to indicate that it is of relatively recent origin and has not become fully established in the germplasm. It is still in the condition of an organismal rather than a nuclear character. Whatever interpretation is put upon these results, as indicating a return to ancestral conditions or otherwise, it seems difficult to escape the conclusion that functional inheritance has taken place in these experiments[1], even if the gradual transition be looked upon as a reversion. Nevertheless, one can scarcely suppose that evolutionary adaptation takes place at any such rapid rate.

It is at any rate an advantage that the subject of inheritance of acquired characters is emerging from neglect into the region of critical experiment, and the attitude with regard to it is becoming less dogmatic and more cautious. Darwin found no difficulty in accepting both the Lamarckian and selection factors as contributory to evolution. We are endeavouring to show that from the point of view of our present knowledge of organic structure the neo-Lamarckian and mutation factors are not incompatible or mutually exclusive.

A recent paper which is of interest because it frankly subsumes the neo-Lamarckian factor (Roberts, 1919), developes the hypothesis that mechanical reaction to stress is the law in all tissues. Just as the flying buttresses of a Gothic cathedral were the result of an effort to shore up walls which were spreading under the increased

[1] MacBride (1919) upholds Kammerer's contention. Bateson (1919) in a reply points out that the fingers in the photograph of the control frog in Kammerer's paper have been clumsily retouched or painted over, and that the critical photograph showing the Brunftschwielen of the modified male shows what appears to be a sort of excrescence on the outside of the fourth finger of the right hand. This, however, does not alter the evidence for the presence of a Brunftschwiele, which is clearly shown in the photograph as a lump on the right wrist. Moreover, a series of nine histological drawings from sections of the horny pad are given, showing the details of structure of this region in males of Alytes in which it is wholly or partly developed, also during the breeding and resting seasons, and in females. These drawings must either be regarded as evidence, in which case they prove Kammerer's point, or treated as deliberate frauds. There seems no sufficient reason for adopting the latter alternative, but it is certainly to be expected that Dr. Kammerer will now be able to produce specimens showing the horny pad.

weight of the roof; so alternate breakdown and repair have led to the present structural relationships in many parts of the human body. Thus the heart is described as an aneurism, and the stomach as a dilatation sac, whose thick muscular wall has developed as the result of disaster and repair. It is assumed that the transmission of these changes probably takes place by a morphogenetic reply *in utero* to increased functional stresses.

Brief mention must be made of the important work of Harrison (1920a) on melanism and other racial characters in certain Geometrid moths. After intensive observation and experiment with the genus Oporabia, Harrison concludes that the subspecies *O. filigrammaria* was evolved from *O. autumnata* during the Glacial period by the action of changed climatic conditions, and that "almost certainly" many of the racial and subspecific differences are "true Lamarckian effects," in particular the food instincts in *O. filigrammaria* and the period of emergence of the pinewood race of *O. autumnata*. Moreover, a Lamarckian explanation of melanism is considered necessary, the darkening resulting from metallic salts in the food, derived from the smoke in industrial areas and from sea fogs in coastal areas where melanism frequently occurs. Melanism is known to behave as a simple Mendelian dominant in many species (see *e.g.*, Onslow, 1920). Harrison (1920b) has recently shown this to be true of the melanic variety of *Tephrosia crepuscularia* when crossed with the type, out in interspecific crosses between *T. crepuscularia* and *T. bistortata* a chaotic series of F_2 and F_3 forms was obtained, the behaviour being no longer describable in Mendelian terms. This recalls the result obtained by the writer (1915f) in crosses between the Mendelian dominant character in *Œnothera rubricalyx* and another species, *Œ. grandiflora*. In both cases dilution and modification of the character has resulted from crossing with a different species. If crossing will modify such a unit-factor, then it is not unreasonable to suppose that they may be capable of environmental modification.

If the Lamarckian explanation of melanism is a true one, then it would appear to be a case of parallel induction, because of its manner of inheritance in crosses, indicating that the nuclear structure is already altered. The function of hormones as an evolutionary means of handing on or accelerating modifications, as suggested by Cunningham (1908), Dendy (1911) and others, indicates a method by which modifications may be perpetuated until the change becomes germinal by producing an alteration in the nucleus.

This is obviously a field where more definite conceptions will only be possible after much further experimental work.

To mention a single case of experimental morphogenesis in plants, Harper (1918) has carefully studied the organization and reproduction of Pediastrum colonies, and concludes that from the point of view of inheritance the characters are of different kinds. The four-lobed shape of the cells of a colony he thinks may be an adaptive character which arose as an environmental response to the pressure relations between cells and has now become fixed and transmitted by cell division.

In the ostrich[1] there are two callosities on the ankle, one median which appears before hatching, hence inherited; the other on the side, which appears only after the bird uses this surface to rest upon and is not transmissible. It is indicated that the median callosity is much older, dating back to the Pliocene ostrich, which, having three toes, rested on its legs symmetrically and so developed the median callosities which have since become inherited independently of any external stimulus. This callosity is no longer used, the loss of the third toe, according to Duerden, having led to a shifting of the point of contact with the ground and the development of a new callosity which is not transmitted. The difference in inheritance of these two callosities is very difficult to explain satisfactorily on any basis except that of functional inheritance.

Brief reference must also be made to two important papers by Guyer and Smith[2] recently received. A fowl serum was prepared sensitized to (*i.e.*, containing a cytolysin which dissolved) the lens of the eye of the rabbit. This serum injected into pregnant rabbits produced inherited defects in the eyes of many of the young. Experiments with mice gave similar results. In rabbits the defects were transmitted for six generations, through the male as well as the female, and were gradually intensified without any further injections. The defect behaved in general as a Mendelian recessive. Here is clearly a specific modification produced by extrinsic factors.

In concluding this chapter, it is evident that conceptions of functional inheritance in various forms are again making themselves felt in much of the constructive thinking of the present time.

[1] Duerden, J. E. Amer. Nat. Vol. 54, 1920.

[2] Journ. Exptl. Zool. Vols. 26, 31.

CHAPTER XI.

General Comparison of Recapitulatory and Karyogenetic Characters.

The Biogenetic Law.

It is only necessary to refer to two recent discussions of the biogenetic law in addition to those already cited. In his excellent book on form and function, Russell (1916) has written a history of animal morphology, including numerous references to the biogenetic law. Those who have opposed the law appear to have based their beliefs largely on (1) the dissimilarities found in related embryos and eggs, (2) the fact that specific characters often make their appearance very early in the ontogeny. Now both these situations are to be anticipated if mutations have taken place in organisms which already display recapitulatory characters. One of the most striking cases of the appearance of specific characters very early in the ontogeny, is cited by Russell (l.c., p. 352), who quotes Louis Agassiz. The latter wrote in 1859 that the snapping turtle " exhibits its small cross-like sternum, its long tail, its ferocious habits, even before it leaves the egg, before it breathes through lungs." It snaps at everything brought near, even when still surrounded by its amnion and allantois. This is to be expected if the specific characters in question have originated through mutations, for it is now well-proven, in plants at least that mutational characters begin to express themselves very early in the ontogeny. And this is a natural result of the circumstance that they are present in every nucleus. On the other hand, there is a certain amount of embryological evidence in animals that characters borne in the nuclei (in contrast to morphogenetic substances in the egg cytoplasm) frequently became actuated only after the earlier cleavage stages are passed. That such characters make their first appearance earlier than some of the recapitulatory characters which they traverse, is also to be expected; but it only limits and does not nullify the biogenetic law, since that law applies only to recapitulatory characters but not to ordinary mutational characters.

Sedgwick's (1894) criticisms of von Baer's law are based on the same objections as those considered above. He compared the embryos of the fowl and dogfish, admitting that they agree in many important points, as the presence in the chick of pharyngeal clefts, a tubular piscine heart, a similar arrangement of the cardiac

arterial system, a cartilaginous endo-skeleton, oro-nasal grooves and a notochord. But he finds "equally important differences." Nevertheless, he admits the essential point for recapitulation—that embryos pass through "stages of structure permanent in lower members of the same group." He also says (p. 43), "The evidence seems to indicate that in a number of cases adult variations of any part are accompanied by precedent similar alteration of the same part in the embryo." We have already seen that this is accounted for on a mutational basis.

It is well-known that Hyatt showed with fossil Ammonites that there is recapitulation in successive coils of the shell, the first coils often reproducing characters belonging to types known from the palæontological record to be ancestral. His law of acceleration in development, deduced from purely palæontological observations is simply another expression of the more recent embryological law of tachygenesis.

Morgan (1916, p. 19) has recently expressed the view that the new mutationist ideas have played havoc with the biogenetic law. He says, for example, that the chick, the fish, and man all possess gill-slits at an early stage of their development merely because they have not lost them. But this merely glosses over a difficulty without explaining it. The fallacy in such an explanation is evident enough if one applies it to such a recent recapitulation as that of the parasitic Copepod, Achtheres (see page 232). In such a case the *larval* stage of this copepod corresponds obviously to the *adult* stage of free-living copepods. Achtheres, however, passes through and beyond this stage, and *its* adult stage has lost practically all its copepod features. We venture to think this is a recapitulatory phenomenon, involving a lengthening of the life-cycle and probably also the inheritance of acquired characters.

Relation to Geographic Distribution.

Brief allusion only will be made to this subject. We have already seen that recapitulatory characters appear to involve a gradual adaptation to a new habitat, while mutations do not. In this connection we have pointed out (Gates, 1917c) another relationship between variation and geographic distribution. With reference particularly to North American owls (*Otus asio*), it was shown that in Eastern North America the red colour phase, which occurs usually in the same regions as the gray with which it interbreeds, probably originated as a mutation and behaves as a dominant Mendelian character. In Western America, on the other hand, a

series of geographic sub-species succeed each other down the Pacific coast, the most northern form being largest and with dark brown markings, while further south they become progressively smaller and lighter in colour, *i.e.*, with less brown and more gray. These various sub-species are co-terminous with each other in their distribution and they form a very close, practically continuous series. The conclusion was reached that while such discontinuous variations as the red colour phase are independent of environmental or functional influence, the continuous type occupying distinct and adjacent geographic areas, represents the results of the stress of environment on the species in its dispersal, leading to the gradual differentiation of local races or sub-species.

Sumner (1918), in his studies of the deer mice, *Peromyscus maniculatus*, has arrived at similar conclusions regarding the occurrence of both mutations and gradual differentiations, and their geographic relationships. This subject is one which requires much further investigation, but it is at least possible that this continuous type of geographic variety in its origin involves the neo-Lamarckian factor.

The neo-Lamarckian principle.

Experiments have shown that impressed modifications may affect the offspring for at least two generations, and to this extent the neo-Lamarckian principle has already been justified. The mechanism of transmission in such a case is apparently different from that of a mutation or a Mendelian character in a cross. The latter appears to be determined in the nuclei, and therefore transmitted as a stable and permanent feature. The acquired character is temporary, cytoplasmic in origin, and will not be permanently retained unless re-impressed generation after generation until the nuclei of the germ cells are ultimately altered in their constitution.

The fixation of such an organismal character may require a longer or shorter number of generations. What determines the number of generations required is quite unknown at the present time, nor is the *modus operandi* understood. But we may assume that in the process, altered metabolic products in the cytoplasm ultimately produce a modification of a chromatin element which is permanent in character. It may be expected that such a transformation will occur much more rapidly in some cases than others.

The views here set forth regarding the occurrence of both mutational and adaptational characters in organisms are entirely in harmony with Dendy's (1913, 1916) conclusions from investigations of the sponges. He concludes that the specific characters of sponges are generally non-adaptive, and that a great many of the spicule differences so characteristic of the group must have originated by mutations. He also points out what we would now regard as parallel mutations, as in the appearance of trichodragmata, and in the polyphyletic family Epipolasidæ, which is an assemblage of stelletid sponges which have independently lost their triæne spicules. Usually the most minute differences, both in megascleres and microscleres, remain constant throughout the species, though millions of spicules may occur in each individual, to whom these microscopic differences cannot be of the slightest use. Such differences point to chemical or physical alterations in the constitution of the germplasm.

On the other hand, adaptive modifications of spicules for various purposes have taken place, as in the modification of triænes into grapnels for anchoring the sponge to a muddy bottom, or into discotriænes which serve as a dermal protection. Some of these adaptive conditions may have come about through selection among a series of mutations, but it is difficult to see that any of them involve the principle of inheritance of acquired characters.

CHAPTER XII.

Orthogenetic Characters.

In previous chapters we have drawn a contrast between (a) karyogenetic characters originating as mutations in the germplasm and affecting every nucleus, and (b) organismal characters which belong to the organism as a whole, show recapitulation, and probably originate as environmentally impressed modifications of the cytoplasm. In this chapter we wish to consider briefly orthogenetic characters, which appear to stand midway between these two categories. Like the former they are germinal in origin, and like the latter they show recapitulation. But they differ from the recapitulatory characters previously considered, in that their origin is apparently not adaptational but on the contrary independent of environment. We will refer only to three cases from the recent experimental work with animals.

It is a well-known fact that in many birds the juvenile plumage differs from that of the adult, and usually at least represents a less specialized and presumably ancestral type of plumage. One of the most striking cases, recently studied by Beebe (1914), is in the white ibis, *Guara alba*. In the young chick the head and neck are covered with black down, becoming smoky gray over the greater part of the body except the under parts, which are white. In the juvenile and post-juvenile stages this is gradually replaced by white feathers, until late in the second year the birds are pure white with scarlet legs and bill. It seems clear that such a white bird has not originated through a mutation, and that the ontogeny represents a gradual transition from a dark-coloured ancestor. It is an interesting fact that the white loral spots in the young chick, which quickly disappear, apparently represent the permanent facial marking of a related ibis, *Plegadis autumnalis*. This would appear to be one of the few cases in which a specific (generic) difference is at the same time a recapitulatory character.

Whitman's (1919) recent posthumous volumes on orthogenetic evolution in pigeons cite a number of cases of juvenile plumage as recapitulatory stages furnishing evidence of orthogenetic development. Whitman's study of the wing patterns of pigeons is perhaps the most prolonged and intimate investigation which has ever been made of a single character. Reading the series in the opposite direction from Darwin, he concluded that the primitive condition was a uniform chequered pattern covering the whole wing, as in

the Japanese turtle dove. Then he shows how in different groups of wild species of pigeons from all over the world, various stages of the reduction of this pattern are found, beginning always at the anterior end of the wing and wiping off the rows of spots until, in unrelated species belonging to different groups, patterns with 4, 3, 2, 1 or no bars of spots may be found. The rock pigeon (*Columba livia)* with usually two wing-bars thus represents a relatively reduced condition, while the white-winged pigeon (*Melopelia leucoptera*), in which the chequers have entirely disappeared, is a still more advanced stage. In these cases, moreover, the juvenile plumage generally represents the more extensively chequered and primitive type, recapitulation thus strongly supporting the author's interpretation. Whitman further claims that this orthogenetic trend in the colour patterns of pigeons is not a mere result of selection, but may even run counter to it and gradually eliminate a pattern of spots which sexual selection tended to strengthen and beautify. His monumental work places in a new light the claims of orthogenesis as an evolutionary factor, but space forbids a more extensive discussion of his results.

The claims of orthogenesis have also been taken up recently by Duerden (1919) for the ostriches. He believes that the reduction in the plumage, in the toes and their scutellation, and in other features, is proceeding progressively and independently in the North and South African ostrich. He believes the evidence is clear that the progress is entirely independent of adaptational considerations. On the other hand, there seems no doubt of the germinal origin of many of the variations. The case of reduction in toes and specialization of the middle toe for running is in many respects similar to that of the horse. If that is so, adaptation would appear to have taken place by the progressive selection of germinal variations. It does not necessarily follow, as Duerden believes, that the reduction of the ostrich's toes will continue until the extinction of the species results.

The last five chapters have been devoted to an attempt to bring into relation with each other such diverse things as the mutation theory, the cell theory, the facts of recapitulation and the evidence for the inheritance of acquired characters. We found that new features of the organism may originate internally through chromatin changes and express themselves centrifugally in the ontogeny of the organism; or they may originate externally as organismal characters and ultimately become inherited, through a

centripetal effect on tbe nuclei. We also concluded that karyogenetic characters were not as a rule recapitulatory, because they imply a change in the nuclear unit which is transmitted by mitosis to every cell, while organismal characters may become so by adding on certain stages to the life-cycle of the organism. The existence of these two types of characters accounts for many anomalies in the biogenetic law. The existence of two such classes of characters makes it possible to understand better many features of organic structure and inheritance.

But it is obvious that the relationship between these two types of characters cannot be fully understood in all their aspects at the present time, nor can a sharp line always be drawn between karyogenetic, cytogenetic and orthogenetic characters—in some aspects they shade into each other. As a constructive attempt to harmonize two bodies of evidence which are obviously in conflict and have long been considered irreconcilable, we make no apology for its tentative character and incompleteness.

LITERATURE CITED.

Agar, W. E., 1913. Transmission of environmental effects from parent to offspring in *Simocephalus vetulus*. Phil. Trans. Roy. Soc., B. 203 : 319 350.

Allen, Charles E., 1919. The basis of sex inheritance in Sphærocarpos. Proc. Amer. Phil. Soc., 58 : 289-316, figs. 27.

Balfour, Bayley, 1917. Observations on Rhododendron seedlings. Trans. and Proc., Bot. Soc., Edin. 27 : 221-227.

Bartlett, H. H., 1914a. An account of the cruciate flowered Œnotheras of the sub-genus Onagra. Amer. Journ. Bot. 1 : 226-243, figs. 2, pls. 19-21.

,, ,, 1914b. Twelve elementary species of Onagra. Cybele Columbiana 1 : 37-56, pls. 5.

,, ,, 1915a. Mutation "en masse." Amer. Nat. 49 : 129-139, figs. 9.

,, ,, 1915c. The mutations of *Œnothera stenomeres*. Amer. Journ. Bot. 2 : 100-109, figs. 4.

,, ,, 1915e. Systematic studies on Œnothera, 5. Rhodora 17 : 41-44, pl. 3.

Bateson, W., 1909. Mendel's principles of heredity. Cambridge University Press, pp. 396, figs. 37, pls. 6.

,, 1913. Problems of Genetics. Oxford University Press, pp. 258, figs. 13, pls. 2.

,, 1919. Dr. Kammerer's testimony to the inheritance of acquired characters. Nature 103 : 344-5.

,, and E. R. Saunders, 1902. Experimental studies in the physiology of heredity. Reports of Evolution Committee, Royal Society, Report I. pp. 160.

, and Ida Sutton, 1919. Double flowers and sex linkage Begonia. Journ. Genetics, 8 : 199-207, pl. 8.

Baur, E., 1911. Einführung in die experimentelle Vererbungslehre. Berlin: Borntræger, pp. 293, figs. 80, pls 9.

Beebe, C. William, 1914. Notes on the ontogeny of the white ibis, *Guara alba*. Zoologica 1: 241-248, fig. 97.

Blackman, V. H., 1909. Alternation of generations and ontogeny. New Phytol. 8: 207-218.

Bonavia, E., 1895. Studies in the evolution of animals. London: Constable, pp. 362, figs. 128.

Boulenger, G. A., 1897-98. The tailless Batrachians of Europe. London, Ray Society, pp. 376, pls. 24, figs. 124.

,, ,, 1918. Sur les rapports de l'ontogenie à la taxinomie chez les Batraciens anoures. Comptes R. Acad. Sci., Paris, 167: 60-63.

,, ,, and N. Annandale, 1918. Further observations on *Rana tigrina*. Rec. Ind. Mus. 15; 51-67, figs. 3.

Bower, F. O., 1908. The Origin of a Land Flora. London: Macmillan, pp. 727, figs. 361.

Braun, Hermann, 1909. Die spezifischen Chromosomenzahlen der einheimischen Arten der Gattung Cyclops. Arch. f. Zellforsch. 3: 449-482, pls. 24-5, figs. 2.

Bridges, Calvin B., 1916. Non-disjunction as proof of the chromosome theory of heredity. Genetics 1: 1-52, 107-163, figs. 9, pl. 1, tables 86.

,, ,, 1917. Deficiency. Genetics 2; 445-465.

Cockayne, L. A., 1907. On the sudden appearance of a new character in an individual of *Leptospermum scoparium*. New Phytol. 6: 43-46.

Cockerell, T. D. A., 1912. The red sunflower. Pop. Sci. Monthly: 373-382.

,, ,, 1915. Specific and varietal characters in annual sunflowers. Amer. Nat. 49: 609-622, figs. 2.

,, ,, 1919a. The varieties of *Helianthus tuberosus*. Amer. Nat. 53: 188-192, figs. 2.

,, ,, 1919b. The girasole or Jerusalem artichoke. Monthly Bull. State Comm. Hort. 8: 1-8, figs. 7.

Conklin, E. G., 1916. Heredity and environment in the development of men. Princeton Univ. Press, 2nd Ed., pp. 550, figs. 96.

Coulter, John M., 1915. Orthogenesis in plants. Science N.S. 42: 683.

,, ,, and C. J. Chamberlain, 1910. Morphology of Gymnosperms. University of Chicago Press, pp. 458, figs. 462.

Crampton, H. E., 1917. Studies on the variation, distribution and evolution of the genus Partula. The species inhabiting Tahiti. Publ. Carnegie Inst. Wash., No. 228. pp. 313, pls. 34, figs. 7.

Cunningham, J. T., 1908. The heredity of secondary sexual characters in relation to hormones, a theory of the heredity of somatogenic characters. Arch. f. Entw.-Mech. 26: 372-428.

Davenport, C. B., 1914. The bare necks. Journ. of Heredity 5: 374, fig. 1.

Davis, B. M., 1909. Pollen development of *Œnothera grandiflora*. Ann. of Botany 23: 551-571, pls. 2.

,, ,, 1913. The behaviour of hybrids between *Œnothera biennis* and *Œ. grandiflora* in the second and third generations. Amer. Nat. 47: 449-476, 547-571, figs. 17.

,, ,, 1914. Parallel mutations in *Œnothera biennis* L. Amer. Nat. 48: 498-501.

,, 1916. Life histories in the red algæ. Amer. Naturalist 50: 502-512.

Davis, B. M., 1918. The segregation of *Œnothera brevistylis* from crosses with *Œnothera Lamarckiana*.
Genetics 3 : 501-533, figs. 7.

Delaunay, L., 1915. Etude comparée caryologique de quelques espèces du genre Muscari Mill. [Russian].
Mém. Soc. Nat. de Kiev 25 : 33-61, pl. 1, figs. 2.

Dendy, Arthur, 1911. Momentum in evolution.
Report Brit. Assoc., Portsmouth Meeting.

,, ,, 1913. By-products of organic evolution.
Journ. Quekett Micro. Club 12: 65-82, pl. 1.

,, ,, 1916. Some factors of evolution in sponges.
Journ. Quekett Micro. Club 13 : 27-46.

De Vries, Hugo, 1909. The mutation theory. Vol. I. English Trans., Chicago : Open Court Publ. Co., pp. 582, figs. 119, pls. 6.

,, ,, 1913. Gpuppenweise Artbildung, unter spezieller Berücksichtigung der Gattung Œnothera.
Berlin: Gebruder Borntraeger, pp. 365, figs. 121, pls. 22.

,, ,, 1915a. *Œnothera gigas nanella*, a Mendelian mutant.
Bot. Gazette 60 : 337-345.

,, ,, 1915b. The coefficient of mutation in *Œnothera biennis* L.
Bot. Gazette 59 : 169-196.

,, ,, 1916. New dimorphic mutants of the Œnotheras.
Bot. Gazette 62 : 249-280, figs. 5.

,, ,, 1918. Mutations of *Œnothera suaveolens* Desf.
Genetics 3 : 1-26, figs. 4.

,, ,, 1919. *Œnothera Lamarckiana erythrina* eine neue Halbmutante.
Zeits. f. Abst. u. Vererb. : 21 : 91-118.

Domin, Karl, 1908. Studien zur Entstehung der Arten durch Mutation I.
Beih. z. Bot. Centralbl. 23 : 15-25, pls. 2, figs. 2.

Doncaster, L., 1920. An introduction to the study of Cytology. Cambridge University Press, pp. 280, pls. 24, figs. 31.

Duerden, J. E., 1919. Crossing the North African and South African ostrich.
Journ. of Genetics, 8: 155-198, pl. 7, figs. 2.

Eames, A. J., 1913. The morphology of *Agathis australis*.
Ann. of Botany, 27 : 1-38, pls. 4, figs. 92.

East, E. M. and D. F. Jones, 1919. Inbreeding and outbreeding: their genetic and sociological significance. Philadelphia and London : Lippincott, pp. 285, figs. 46.

Farmer, J. Bretland and L. Digby, 1907. Studies in apospory and apogamy in ferns. Ann. of Botany, 21 : 161-199, pls. 5.

Fernald, M. L., 1917. A remarkable colony of Bidens in Connecticut.
Rhodora, 19 : 257-259.

Fraser, H. C. I. and J. Snell, 1911. The vegetative divisions in *Vicia Faba*.
Ann. of Botany, 25 : 845-855, pls. 2.

Fritch, F. E., 1916. The algal ancestry of the higher plants.
New Phytol., 15: 233-250, figs. 2.

Frost, H. B., 1912. The origin of an early variety of Matthiola by mutation.
Proc. Amer. Breeders' Assoc. 7 : 536-545.

,, 1915. The inheritance of doubleness in Matthiola and Petunia.
Amer. Nat. 49 : 623-636, fig. 1.

Gates, R. R., 1909a. The stature and chromosomes of *Œnothera gigas* de Vries.
Arch. f. Zellforsch. 3 ; 525-552.

,, 1909b. Further studies of Œnotheran cytology. Science N.S. 29 : 269.

1911. Studies on the variability and heritability of pigmentation in Œnothera. Zeitschr. f. Abst. u. Vererb. 4: 337-372, pl. 6, figs. 5.

Gates, R. R., 1912a. Parallel mutations in *Œnothera biennis*. Nature, 89: 659-660.

„ 1912b. Somatic mitoses in Œnothera. Ann. of Botany, 26: 993-1010, pl. 1.

„ 1913. A contribution to a knowledge of the mutating Œnotheras. Trans. Linn. Soc., 2nd Ser, Botany, Vol. 8, Part I., pp. 67, pls. 6.

„ 1914a. Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. f. Abst. u. Vererb. 11; 209-279, figs. 25.

„ 1914b. Some Œnotheras from Cheshire and Lancashire. Ann. Mo. Bot. Gardens 1: 383-400, pls. 3.

„ and Nesta Thomas, 1914. A cytological study of *Œnothera* mut. *lata* and *Œ*. mut. *semilata* in relation to mutation. Quart. Journ. Micro. Sci. 59: 523-571, pls. 3, figs. 4.

„ 1915a. The Mutation Factor in Evolution, with particular reference to Œnothera. London: Macmillan, pp. 353, figs. 114.

„ 1915b. On successive duplicate mutations. Biol. Bull.: 29: 204-220.

„ 1915c. Heredity and mutation as cell phenomena. Amer. Journ. Bot. 2: 519-528.

„ 1915d. On the nature of mutations. Journ. of Heredity 6: 99-108, figs. 7.

„ 1915e. On the origin and behaviour of *Œnothera rubricalyx*. Journ. of Genetics 4: 353-360.

„ 1915f. On the modification of characters by crossing. Amer. Nat. 49: 562-569.

„ 1916. On pairs of species. Bot. Gazette 61: 177-212, figs. 12.

„ 1917a. Vegetative segregation in a hybrid race. Journ. of Genetics 6: 237-253, pl. 1.

„ 1917b. A systematic study of the North American genus Trillium, its variability, and its relation to Paris and Medeola Ann. Mo. Bot. Garden 4; 43-92, pls. 3.

„ 1917c. The mutation theory and the species concept. Amer. Nat. 51: 577-595, fig. 1.

„ 1918a. A systematic study of the North American Melanthaceæ from the genetic standpoint. Journ. Linn. Soc., Botany 44: 131-172, pl. 1.

„ 1918b. A systematic analytical study of certain North American Convallariaceæ, considered in regard to their origin through discontinuous variation. Ann. of Botany 32: 253-257.

Geerts, J. M., 1907. Über die Zahl der Chromosomen von *Œnothera Lamarckiana*. Ber. deut. bot. Gesells. 25: 191-195, pl. 1.

Glen, Edith H., 1918. A revision of certain points in the early development of *Peripatus capensis*. Quart. Journ. Micro. Sci. 63: 283-292, pl. 1.

Gudernatsch, J. F., 1914. Feeding experiments on tadpoles, II. A further contribution to the knowledge of organs with internal secretion. Amer. Journ. Anat. 15: 431-480, pls. 2.

Gulick, J. T., 1905. Evolution, racial and habitudinal. Carnegie Inst. of Wash., Publ. No. 25, pp. 269, pls. 3.

Hance, Robert T., 1918. Variations in the number of somatic chromosomes in *Œnothera scintillans*, De Vries. Genetics 3: 225-275, pls. 7, figs. 5.

Harper, R. A., 1918. Organization, reproduction and inheritance in Pediastrum. Proc. Amer. Phil. Soc. 57: 375-439, pls. 2, figs. 35.

Harrison, J. W. Heslop, 1920a. Genetical studies in the moths of the Geometrid genus Operabia (Oporinia) with a special consideration of melanism in the Lepidoptera. Journ. of Genetics 9: 195-280, figs. 13.

Harrison, J. W. Heslop, 1920b. The inheritance of melanism in the genus Tephrosia (Ectropis) with some consideration of the inconstancy of unit characters under crossing. Journ. of Genetics 10: 61-85, figs. 3.

Heribert-Nilsson, N , 1912. Die Variabilität der *Œnothera Lamarckiana* und das Problem der Mutation. Zeits. f. Abst. u. Vererb. 8: 89-231, pls. 3, figs. 36.

Hilbert, R., 1913. *Hepatica triloba* Gil. mit gefüllter Blüte. Allgem. Bot. Zeitschr. f. Syst. Floristik, etc. 19: 140-142.

Hooper, J. J., 1916. A peculiar breed of goats. Science N.S. 43: 571.

Howard, A. and G. L. C. Howard, 1912. On the inheritance of some characters in wheat. Mem. Dept. Agr., India (Botany), 5: 1-46, pls. 3.

Hus, Henri, 1911. The origin of species in nature. Amer. Nat. 45: 641-667, figs. 7.

Hutchinson, A. H., 1915. On the male gametophyte of *Picea canadensis.* Bot. Gazette 59: 287-300, pls. 5.

Hyde, R. R., 1915a. The origin of a new eye-color in *Drosophila repleta*, and its behavior in heredity. Amer. Nat. 49: 183-185.

,, 1915b. A wing mutation in a new species of *Drosophila.* Amer. Nat. 49: 185-187.

Jeffrey, E. C., 1917. The anatomy of woody plants. University of Chicago Press. Pp. 478, figs. 306.

Kammerer, P., 1909. Vererbung erzwungener Fortpflanzungsanpassungen. III. Die Nachkommen der nicht brutpflegenden *Alytes obstetricans.* Arch f. Entw. Mech. 28: 447-545, pls. 2.

,, ,, 1919. Vererbung erzwungener Formveränderungen. I. Die Brunftschwiele des Alytes Männchen aus "Wassereiern." Arch. f. Entw. Mech. 45: 323-370.

Keeble, F., C. Pellew, and Jones, W. N., 1910. The inheritance of peloria and flower-colour in foxgloves (*Digitalis purpurea*). New Phytol. 9: 68-76.

Lang, Arnold, 1912. Vererbungswissenschaftliche Miszellen. Zeits. f. Abst. u. Vererb. 8: 233-283, figs. 6.

Lang, W. H., 1898. On apogamy and the development of sporangia upon fern prothalli. Phil. Trans. Roy. Soc., London B. 190: 187-238, pls. 5.

,, 1901. On apospory in *Anthoceros lævis.* Ann. of Botany 15: 503-510, pl. 1.

,, 1909. A theory of alternation of generations in Archegoniate plants based on ontogeny. New Phytol. 8: 1-12.

Lewis, I. F., 1909. The life history of *Griffithsia Bornetiana.* Ann. of Botany 23: 641-690, pls. 5, figs. 2.

Lodewijks, J. A., 1911. Erblichkeitsversuche mit Tabak. Zeitsch. f. Abst. u. Vererb. 5: 139-172, figs. 9.

Loeb Jacques, 1916. The Organism as a whole. Putnams: New York and London, pp. 379, figs. 51.

Lutz, Anne M., 1908. Chromosomes of the somatic cells of the Œnotheras. Science N.S. 27: 335.

,, 1909. Notes on the first generation hybrid of *Œnothera lata* × *Œ. gigas.* Science N.S. 29: 263-267.

,, 1916. Œnothera mutants with diminutive chromosomes. Amer. Journ. Bot. 3: 502-526, pl. 1, figs. 7.

,, 1917a. Characters indicative of the number of somatic chromosomes present in Œnothera mutants and hybrids. Amer. Nat. 51: 375-377.

,, 1917b. Fifteen- and sixteen-chromosome Œnothera mutants. Amer. Journ. Bot. 4: 53-111, figs. 9.

MacBride, E. W., 1914. Text book of Embryology, Vol. I. Invertebrata, London : Macmillan, pp. 692, figs. 468.

„ „ 1917. Recapitulation as a proof of the inheritance of acquired characters. Scientia 22 : 425-434.

„ „ 1919. The inheritance of acquired characters. Nature 103 : 225-6.

May, H. G., 1917a. The appearance of reverse mutations in the bar-eyed race of Drosophila under experimental control. Proc. Nat. Acad. Sci. 3 : 544-545.

„ 1917b. Selection for higher and lower facet numbers in the bar-eyed race of Drosophila and the appearance of reverse mutations. Biol. Bull. 33 : 361-395, figs. 8.

Metz, C. W., 1914. A preliminary survey of five different types of chromosome groups in the genus Drosophila. Journ. Exptl. Zool. 17 : 45-59, pl. 1.

„ and Metz, B. S., 1915. Mutations in two species of Drosophila. Amer. Nat. 49 : 187-189.

„ 1916a. Linked Mendelian characters in a new species of Drosophila. Science N.S. 44 : 431-2.

„ 1916b. Mutations in three species of Drosophila. Genetics 1 : 591-607, fig. 1.

„ 1916c. The paired association of chromosomes in the Diptera, and its significance. Journ. Exptl. Zool. 21 : 213-262, pls. 8.

„ „ 1916d. Additional types of chromosome groups in the Drosophilidæ. Amer. Nat. 50 : 587-599, pl. 1.

„ „ 1918. The linkage of eight sex-linked characters in *Drosophila virilis*. Genetics 3 : 107-134, pl. 1.

„ „ 1920. Correspondence between chromosome number and linkage groups in *Drosophila virilis*. Science N. S. 51 : 417-418.

Miyoshi, M., 1910. Ueber das Vorkommen gefüllter Blüten bei einem wildwachsenden japanischen Rhododendron, nebst Angabe über die Variabilität von *Menziesia multiflora* Maxim. Journ. Coll. Sci., Tokyo, Vol. 27, Art. 11, pp. 13, pls. 3.

„ „ 1916. Die Japanische Bergkirschen, ihre wildformen und Kulturrassen. Journ. Coll. Sci. Imp. Univ., Tokyo 34 : 1-175, pls. 23, fig. 1.

Morgan, T. H., Sturtevant, Muller and Bridges, 1915. The mechanism of Mendelian heredity. London, Constable, pp. 262, figs. 64.

„ 1916. A critique of the theory of evolution. Princeton University Press, pp. 197, figs. 95.

„ 1919. The physical basis of heredity. London : Lippincott, pp. 305, figs. 117.

Morse, Withrow, 1918. Factors involved in the atrophy of the organs of the larval frog. Biol. Bull. 34 : 149-166, figs. 2.

Müller, H. A. Clemens, 1912. Kernstudien an Pflanzen. Arch. f. Zellforsch. 8 : 1-51, pls. 2.

Muller, H. J., 1917. An Œnothera-like case in Drosophila. Proc. Nat. Acad. Sci. 8 : 619-626.

„ 1918. Genetic variability, twin hybrids and hybrids, in a case of balanced lethal factors. Genetics 3 : 422-499, fig. 1.

Nawaschin, S., 1911. Über eine Art der Chromatindiminution bei *Tradescantia virginica*. Ber. deut. bot. Gesells. 29 : 437-449, pl. 1.

Nilsson-Ehle, H., 1909. Kreuzungsuntersuchungen an Hafer und Weizen. Dissertation : Lund., pp. 122.

Nilsson-Ehle, H., 1911. Kreuzungsuntersuchungen an Hafer und Weizen, II. Lunds. Univ. Arsskrift, N.F. Afd. 2, Bd. 7, No. 6, pp. 82.

Onslow, H., 1920. The inheritance of wing colour in Lepidoptera. III. Melanism in *Boarmia consortaria* (var. *consobrinaria* BKH.) Journ. of Genetics 9: 339-346, pl. 1.

Osborn, H. F., 1918. The origin and evolution of life, on the theory of action, reaction and interaction of energy. London: Bell, pp. 322, figs. 135.

Perrier, E. and Gravier, C., 1902. La tachygénèse ou accélération embryogénique, son importance dans les modifications des phénomènes embryogeniques; son rôle dans la transformation des organisms. Ann. des Sci. Nat. Zool. 16: 133-371, figs. 119.

Plough, H. H., 1917. The effect of temperature on crossing over. Journ. Exptl. Zool. 24.

Punnett, R. C., 1919. Note on the origin of a mutation in the sweet pea. Journ. of Genetics 8: 27-31, fig. 1.

Raciborski, M., 1908. *Coreopsis tinctoria* var. *prolifica*: eine ungweckmässige Mutation. Weisner-Festschrift, pp. 417-420.

Rehder, Alfred, 1907. *Rhododendron albiflorum* with double flowers. Bot. Gazette 43: 281-2.

Renner, O., 1919. Zur Biologie and Morphologie der männlichen Haplonten einiges Önotheren. Zeits. f. Bot. 11: 305-380, figs. 32.

Ritter, W. E., 1919. The Unity of the Organism. Boston: Gorham Press, 2 Vols.

Roberts, Morley, 1919. The function of pathological states in evolution. Proc. Zool. Soc., London, 1918: 237-254.

Rosenberg, O., 1918. Chromosomenzahlen und Chromosomendimensionen in der Gattung Crepis. Arkiv för Botanik 15: No. 11, pp. 16, figs. 36.

Russell, E. S., 1916. Form and function. London: Murray, pp. 383, figs. 15.

Sakamura, Tetsu, 1915. Ueber die Einschnürung der Chromosomen bei *Vicia Faba*, L. Bot. Mag. Tokyo 29: 287-300, pl. 1, figs. 12.

Saunders, E. R., 1910. Studies in the inheritance of doubleness in flowers. I. Petunia. Journ. of Genetics 1: 57-69, figs. 5.

" " 1911a. On inheritance of a mutation in the common foxglove *(Digitalis purpurea)*. New Phytol. 10: 47-63, pl. 1, figs. 11.

" " 1911b. Further experiments on the inheritance of "doubleness" and other characters in stocks. Journ. of Genetics 1: 303-376, figs. 2.

" " 1912. On the relation of *Linaria alpina* type to its varieties *concolor* and *rosea*. New Phytol. 11: 167-169.

" " 1913. The breeding of double flowers. IVe. Conf. Internat. de Génétique, 1911, pp. 397-405.

" " 1915a. A suggested explanation of the abnormally high records of doubles quoted by growers of stocks (Matthiola). Journ. of Genetics 5: 137-143.

" " 1915b. The double stock, its history and behaviour. Journ. Roy. Hort. Soc. 40: 450-472.

" " 1916a. On selective partial sterility as an explanation of the behaviour of the double-throwing stock and the Petunia. Amer. Nat. 50: 486-498.

" " 1916b. The results of further breeding experiments with Petunia. Amer. Nat. 50: 548-553.

" " 1916c. On an early mention of the double wallflower *(Cheiranthus Cheiri)*. Journ. Roy. Hort. Soc. 42: 27-34.

Saunders, E. R., 1917. Studies in the inheritance of doubleness in flowers II. Meconopsis, Althaea and Dianthus. Journ. of Genetics 6: 165-184.

,, ,, 1918. On the occurrence, behaviour and origin of a smooth-stemmed form of the common foxglove *(Digitalis purpurea)*. Journ. of Genetics 7: 215-228.

Sax. Karl, 1918. The inheritance of doubleness in *Chelidonium majus*, Linn. Genetics 3: 300-307.

Sedgwick, A., 1894. On the inadequacy of the cell theory of development' and on the early development of nerves, particularly of the third nerve and of the sympathetic in Elasmobranchii. Quart. Journ. Micro. Sci. 37: 87-101.

,, ,, 1894. On the law of development known as von Baer's Law; and on the significance of ancestral rudiments in embryonic development. Quart. Journ. Micro. Sci. 36; 35-52.

Shull, G. H., 1912. Inheritance of the heptandra-form of *Digitalis purpurea* L. Zeitschr. f. Abst. u. Vererb. 6: 257-267, pls. 2

,, ,, 1914a. A peculiar negative correlation in Œnothera hybrids. Journ. of Genetics 4: 83-102, pls. 2.

,, ,, 1914b. Duplicate genes for capsule-form in *Bursa bursa-pastoris*. Zeitschr. f. Abst. u. Vererb. 12: 97-149, figs. 7.

Small, James, 1917-19. The origin and development of the Compositæ. New Phytol. Vols. 16-18.

Sollas, I. B. J., 1914. Note on the offspring of a dwarf bearing strain of guinea pigs. Journ. of Genetics 3: 201-204.

Stomps, Theo. J., 1912. Mutation bei *Œnothera biennis* L. Biolog. Centlbl. 32: 521-535, pl. 1, fig. 1.

,, ,, 1914. Parallele Mutationen bei *Œnothera biennis* L. Ber. deut. bot. Gesells. 32: 179-188.

Sturtevant, A. H., 1915. A sex linked character in *Drosophila repleta*. Amer. Nat. 49: 190-191.

Sumner, F. B., 1915. Genetic Studies of several geographic races of California deer-mice. Amer. Nat. 49: 688-701, fig. 1.

,, ,, 1917. Several color "mutations" in mice of the genus Peromyscus. Genetics 2: 291-300.

,, ,, 1918. Continuous and discontinuous variations and their inheritance in Peromyscus. Amer. Nat. 52: 117-208, 290-301, 439-454, figs. 13.

Thistleton-Dyer, W. T., 1901. Morphological notes. Ann. of Botany 15: 423-425, 547-8, pl. 1.

Tupper, W. W. and Bartlett, H. H., 1916. A comparison of the wood structure of *Œnothera stenomeres* and its tetraploid mutation *gigas*. Genetics 1: 177-184.

Whitman, C. O., 1894. The inadequacy of the cell-theory of development. Biol. Lectures, Woods Holl, 1893: 105-124.

,, ,, 1919. Vol. I. Orthogenetic evolution in pigeons. Carnegie Inst. Wash. Publ., No. 257, pp. 194, pls. 88, figs. 36.

Wilson, E. B., 1909. Studies on Chromosomes V. The chromosomes of Metapodius. A contribution to the hypothesis of the genetic continuity of chromosomes. Journ. Exptl. Zool, 6: 147-205, pl. 1, figs. 13.

,, ,, 1910. Studies on chromosomes VI. A new type of chromosome combination in Metapodius. Journ. Exptl. Zool. 8: 53-78, figs. 5.

Yamanouchi, S., 1906. The life history of *Polysiphonia violacea*. Bot. Gazette 42: 401-449, pls. 10.

NOTES ON FRESHWATER ALGÆ. I—IV.

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[With Two Figures in the Text.]

I.—A New Species of *Pyramimonas*.

During April and May, 1920, a small motile Alga belonging to the genus *Pyramimonas* (family Polyblepharidaceæ of the order Volvocales) was observed in fair quantity among filaments of *Spirogyra* and *Tribonema* in the overflow ditch of a small pond at Quinton, near Birmingham. The Alga appeared to be absent from the pond itself, occurring only in the very shallow water of the ditch, into which, owing to the heavy rains of April, water from the pond had run. The water of the ditch in places was coloured light green owing to the presence of this Alga. On keeping specimens in the laboratory in open tubes and wide-mouthed glass jars the organism always became encysted after 24-36 hours, and eventually died; and attempts to cultivate it in dilute nutrient solutions were also unsuccessful.

The form of the motile cell is very variable, the commonest shape being sub-pyramidal (Fig. 1, A), sharply truncate and slightly 4-lobed at the anterior end, and somewhat tapering towards the posterior extremity. Transitions to shorter forms which are more or less cordate (Fig. 1, B), or even sub-globose were frequent; while on the other hand more elongated sub-cylindrical individuals (Fig. 1, C) were not rare. The widely truncate anterior end is a characteristic feature of all the cells, and when the latter are observed in anterior view this end is sub-quadrate with rounded angles (Fig. 1, D), due to the four anterior lobes. The usual number of these lobes was four, but occasionally only three were seen in anterior view, giving a sub-triangular form to this end of the cell. The anterior lobes are strictly confined to the anterior end of the cell, and are not continued backwards as ridges, or at any rate are continued for only a very short distance, so that the (optical) transverse section for the greater part of the length of the cell is circular. There is a well-marked depression in the centre of the anterior end, and from the base of this depression arise four cilia.

The motion of the cell is always cilia-end foremost, while at the same time the cell rotates about its longitudinal axis in a direction which (the cell being considered as swimming towards the observer) is clockwise.

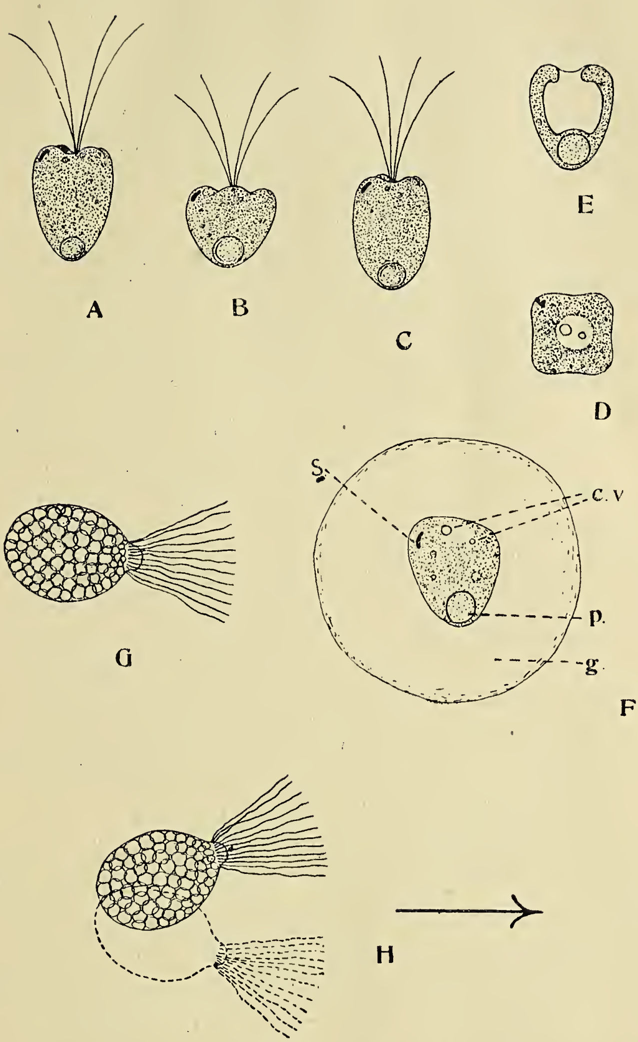


FIG. 1, A—H.

A—C. *Pyramimonas inconstans* sp. n. Various forms of vegetative individuals.

D. Anterior view of motile cell of *P. inconstans*, showing sub-quadrate form, stigma and the two contractile vacuoles (the cilia are not shown).

E. Optical longitudinal section of *P. inconstans*, showing the form of the chloroplast in long. sect., and the basal pyrenoid.

F. Non-motile individual of *P. inconstans*; s. stigma, c.v. the two contractile vacuoles, p. pyrenoid, g. thick hyaline gelatinous investment.

G. Zoogonidium of *Oedogonium cryptoporum*, killed with a drop of dilute iodine solution.

H. Diagram illustrating mode of progression of the zoogonidium of *O. cryptoporum* (described in text).

A—F × 1250; G, H × 900.

There is no cellulose cell-well, the cell being covered with a very delicate protoplasmic membrane, which appears to allow of a certain amount of change of form of the cell. Although such alteration in form was not directly observed in the motile individuals, yet the variability in the shape of the cells seems to be due in part to this power. In the non-motile state, as described below, the cells readily assume various forms, although they generally tend to become sub-globose.

There is a single cup-shaped, bright green chloroplast, occupying practically the whole periphery of the cell, leaving only the centre of the anterior end free and more or less hyaline. The anterior edge of the chloroplast is incurved and slightly thickened, as shown in the optical longitudinal section, Fig. 1, E, while the thickened base of the chloroplast contains a large conspicuous pyrenoid. A rather pale red stigma of elongated form is situated on the outer surface of the chloroplast in the anterior part of the cell, and invariably on the summit of one of the anterior lobes (Fig. 1, A—D), and projecting slightly above the general surface of the cell.

The chloroplast appears to be quite entire at the anterior end. Even under very high powers (a 2 mm. oil-immersion objective was most frequently used in examining the minute structure of the cell), and in cells blistered with a drop of dilute formalin solution, or killed with iodine, or other reagents, the incurved anterior edge of the chloroplast never appeared to be divided into lobes corresponding to the four anterior lobes of the cell.

The pyrenoid has a starch sheath, and minute grains of starch were frequently observed scattered throughout the chloroplast. The addition of a drop of dilute formalin solution causes the cells to become greatly swollen and distorted in the same way as that described by B. M. Griffiths in the case of *Pyramimonas delicatulus*.[1]

Within the chloroplast and in the general cytoplasm of the anterior region of the cell are two (occasionally three) contractile vacuoles. They are very difficult to observe in moving individuals, although occasional glimpses of one or both of them can be obtained. They are more readily seen in the non-motile cells (Fig. 1, F), especially under a high magnification. The period between two successive disappearances of a vacuole is 18—22 seconds. Other small vacuoles were observed in different parts of the cell but these were never observed to pulsate.

[1] B. M. Griffiths. On Two New Members of the Volvocaceæ, New Phytol., VIII, 1909, pp. 130—137.

Under unfavourable conditions the organism readily assumes the "*Palmella*"-state. The cilia are lost and the cells assume various irregular shapes, but generally tend to become more or less sub-globose, the anterior lobes become usually unrecognisable, and the outlines of the chloroplast very indistinct, although stigma and pyrenoid persist, and the contractile vacuoles become more apparent (Fig. 1, F). Around each cell there develops a thick hyaline gelatinous investment (g in Fig. 1, F), and numerous cells often become aggregated together in a common jelly.

These non-motile cells can undergo slow change of form. Griffiths (l.c. p. 134) states that no amœboid alterations in the shape of the cell was observed in *P. delicatulus*, and further remarks that "in this respect *Pyramimonas* appears to differ from the other members of the Polyblepharidaceæ." West,[1] writing of the Polyblepharidaceæ, states that "the body of the cell is invested only by a protoplasmic membrane and, with the possible exception of *Pyramimonas*, is able within prescribed limits to undergo certain changes of form." These two statements concerning *Pyramimonus* are, however, true only in the case of *P. delicatulus*, since Dill in his account of *P. tetrarhynchus* (the third known member of the genus) says "Während der Bewegung sowohl als in der Ruhe konnte ich an diesen Organismen Formveränderungen wahrnehmen." [2] Dill also quotes Dangeard (Le Botaniste 1889, p. 138) as having observed alteration of form ("metabolie") in *P. tetrarhynchus*.

Division of the cell is longitudinal, and takes place in motile as well as non-motile (encysted) individuals, the process of division resembling that described by Griffiths in the case of *P. delicatulus*. It commences at the posterior end of the cell, and gradually extends anteriorly. In the case of motile cells the cilia increase in number to eight prior to cell-division, each daughter cell retaining four.

This species (termed *P. inconstans* on account of the variability in form of the cell) differs from both *P. tetrarhynchus* Schmarda[3] and *P. delicatulus* Griffiths (l. c.) in the smaller size of its cells, the non-lobed chloroplast, and the anterior stigma. From the last-named species it further differs in having no posterior excavation in the chloroplast. The anterior lobes of the cells of *P. inconstans* are also much less developed than those of

[1] West, G. S., Algæ, Vol. I. Camb. Univ. Press, 1916, p. 164.

[2] Dill, O. E., Jahrb. f. wiss. Bot., XXVIII. 1895, p. 344.

[3] Described by Dill, l. c.

either of the other two species. Altogether the cell-structure of the present species is simpler than that of the other two, and for this reason *P. inconstans*, may perhaps be considered as a link connecting these with *Polyblepharis*, which is generally considered as the most primitive genus of the family Polyblepharidaceæ.

The conditions which seem to favour the development of the motile state of *P. inconstans* in nature appear to be (1) relatively dilute pond water, (2) a moderate temperature (about 8°—13° C), and (3) abundant aeration of the water. The last factor seems important when it is considered that the water of the ditch was renewed after each shower by water overflowing from the pond (itself much swollen with rain-water); and also from the fact that motile individuals in a drop of water under a cover-glass all lost their motility in about two hours (probably owing to scarcity of oxygen), while a species of *Chlamydomonus* in the same drop of water was observed to retain its motility for a much longer period.

PYRAMIMONAS INCONSTANS sp. nov. Cellulæ parvæ, plerumque subpyramidatæ sed nonnunquam cordatæ vel subcylindraceæ, polo anteriore late truncato et leviter quadri-lobulato, a vertice visæ subquadratæ (interdum subtriangulæ); chromatophora singularis, viridis, parte anteriore incurvata sed non-lobulata, pyrenoide singulo posteriore instructa; stigma elongatum, in parte anteriore cellulæ situm; vacuolæ contractiles binæ (interdum ternæ).

Long. cell. (8·8)—10—15μ,
lat. cell. 7·5—10μ,
long. ciliorum 13—18μ.

Hab. in fossa, Quinton, prope Birmingham (April and May, 1920).

II. Note on the Zoogonidia of *Oedogonium cryptoporum.*

Some observations were made in March 1919, on the zoogonidia of *Oedogonium cryptoporum*, obtained from Bearwood, near Birmingham. Vegetative specimens of the Alga brought into the laboratory and placed in a large glass vessel of pond water proceeded to form zoogonidia in very large numbers. No mature oogonia were present at that time but later in the spring they matured, and the species was identified as *O. cryptoporum*, Wittr., the record being confirmed by the late Professor G. S. West.

The interesting point about the zoogonidia, hundreds of which were examined, was the length of the cilia. All standard works on freshwater Allgæ appear to agree in describing and figuring the zoogonidia (and also the androgonidia and spermatozoid) of

Oedogonium a having as crown of relatively *short* cilia. Published figures generally show the cilia about $\frac{1}{8}$ to $\frac{1}{4}$ as long as the body of the zoogonidium. The length of the cilia of the zoogonidia of *O. cryptoporum* (Fig 1, G), however, were observed to be $\frac{2}{3}$ to $\frac{4}{5}$ of the body-length, as the measurements given below show.

The zoogonidium of *O. cryptoporum* is oval or subellipsoid in shape, with a prominent hemispherical and hyaline anterior papilla. Fig. 1, G shows the position the cilia always assume when the zoogonidia are killed with a drop of dilute iodine solution. The following are a few measurements of the length of cilia and length of body of the zoogonidium (including the anterior papilla).

Body-length	22·5	20·0	19·7	20·0	21·5	20·0μ
Length of Cilia	15·8	15·5	14·0	16·0	15·5	15·2μ

The relative length of these cilia appears to be markedly greater than that recorded in the motile cells of any other member of the Oedogoniales, as far as can be ascertained from published figures.

The zoogonidia of this species have no eye-spot and are negatively phototactic, always accumulating on the side of the culture-vessel which is turned away from the source of light.

The mode of progression is rather interesting and is represented by Fig 1, H. The arrow gives the general direction in which the zoogonidium is moving, but the longitudinal axis of the latter is never parallel to this direction but makes an angle of about 22·5° with it. Observed under a low magnification the anterior end of the moving zoogonidium appears to oscillate from side to side, but in reality the anterior end describes a circle, the direction of its motion (the zoogonidium being considered as moving towards the observer) being anti-clockwise. In other words the longitudinal axis of the zoogonidium describes a cone, the apex of which is the extreme posterior end of the zoogonidium while the axis of the cone gives the actual direction in which the zoogonidium is moving as a whole.

Occasional zoogonidia of several other (undetermined) species of *Oedogonium* and *Bulbochæte* have been seen at various times, but the relative length of their cilia was always observed to be very much shorter than is the case with those of *O. cryptoporum*. Doubtless, however, this species does not stand alone in having zoogonidia with rather long cilia.

III.—On the Occurrence of "False-branching" in the *Hormidium*-state of *Prasiola crispa.*

As is well-known, the cells of the common filamentous form, or *Hormidium*-state, of *Prasiola crispa* frequently divide by longitudinal as well as transverse walls to form two or more rows of cells (*Schizogonium*-state), which by further divisions produce flat expansions of cells (*Prasiola*-state). True branching in the *Hormidium*-state of this Alga appears to have been recorded only in connection with the production of rhizoids. Wille, for example has described a submarine form of *Prasiola crispa* (termed f. *submarina*[1]) in which certain cells of the filaments had grown out to produce short unicellular rhizoids; only very occasionally did these rhizoidal branches consist of several cells.

Choldat[2] mentions and figures uni- and multi-cellular, simple and also branched, rhizoids in *Schizogonium crispum* (=*Prasiola crispa*). Heering,[3] speaking of the rhizoids of *Prasiola* says: "Selton werden diese Ausstülpungen durch eine Scheidewand von der Mutterzelle abgegrenzt und wachsen zu mehrzelligen Fäden aus."

The writer, however, found pseudo-branching of a character quite different from rhizoid-production in a patch of the *Hormidium*-state of *Prasiola crispa* which occurred on damp ground under a tree in a field at Warley, near Birmingham (in April, 1919). As will be seen from the description below, this pseudo-branching is exactly similar as regards mode of development to the false-branching in the Blue-green algal genera *Tolypothrix* and *Scytonema.*

The mode of development of these pseudo-branches, which were quite frequent and not merely of isolated occurrence in specimens of the Alga from the locality mentioned, is illustrated in Fig. 2, A-D. At intervals along most of the filaments there were short lengths of 1 to 3 (rarely more) dead, apparently empty, and generally much flattened cells (Fig. 2, A).

The living cells on one or both sides of these dead cells, by active division and growth had, in the case of many filaments, pushed their way out through the hyaline sheath surrounding the filament (Fig. 2, B, C.) as short lateral pseudo-branches (Fig. 2, D).

[1] Wille, N., Studien über Chlorophyceen, III, Vid.-Selsk. Skrifter. I. Math.-naturv. Klasse, 1900 (Christiania), pp. 13-18, Taf. 1, Figs. 42-53.

[2] Algues Vertes de la Suisse, Berne, 1902, p. 342, and Fig. 251.

[3] Heering, W., Die Süsswasserflora Deutschlands, Heft. VI, 1914 (Jena), p. 56.

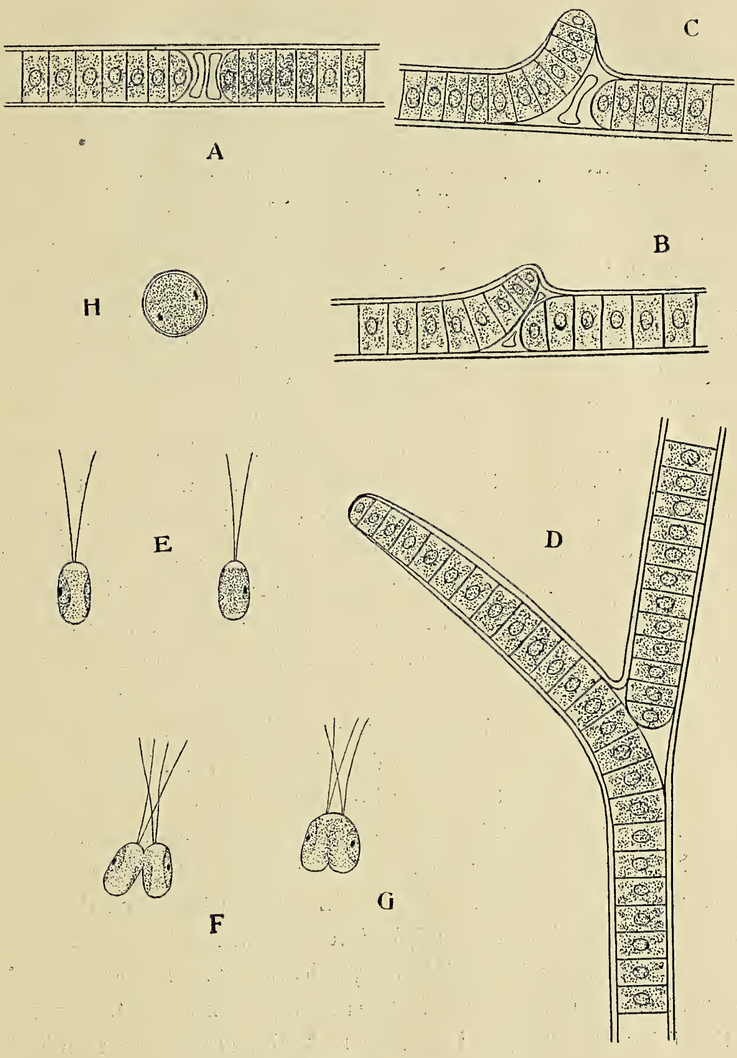


FIG. 2, A—H

A—D *Prasiola crispa*, showing mode of development of pseudo-branches.
A. Two dead and shrivelled cells in a filament.
B, C. Very young pseudo-branches.
D. Older pseudo-branch.
E. Gametes of *Chlamydomonas variabilis* Dang., showing the form of the chloroplast.
F. The same just beginning to fuse.
G. Later stage in process of fusion of the gametes.
H. Zygote, showing the two persistent stigmas.

A—D × 550 ; E—H × 800.

The dead intercalary cells which were generally present at the point in the filament where the false-branches arose, are thus curiously analogous to the heterocysts of *Tolypothrix* and *Scytonema*, in the relation which they bear to the false-branches. The closest resemblance is to *Tolypothrix*, where the pseudo-branches arise singly and the heterocysts are seriate; occasionally, however, in the *Prasiola* the pseudo-branches arose in pairs, one on each side of the dead intercalary cells, thus recalling *Scytonema*.

Several writers have described the occurrence of dead, flattened or biconcave, cells in filaments of the *Hormidium*-state of *Prasiola crispa*. F. E. Fritsch,[1] for example, described and figured such dead cells in specimens of the Alga from the Antarctic, and the dead cells mentioned above in the Warley material appear to be similar to those described by this author.

Occasionally no sign of dead intercalary cells could be seen at the point of origin of the pseudo-branch, and in several cases it was distinctly seen that the latter was given off at a place in the filament where no dead cells were present. Possibly the development of these pseudo-branches in *Prasiola* may be explained by the Alga having gone through a short period unfavourable to growth, which resulted in certain intercalary cells being killed, and their contents disorganised,[2] while, favourable conditions again ensuing, the filaments later resumed active growth and produced the pseudo-branches at places of weakness in the filaments.

The apices of the pseudo-branches always consisted of somewhat narrower and thinner-walled cells, obviously in process of active division and growth. The "branches" were generally short (rarely more than 25 cells in length) but doubtless given favourable conditions they might have grown much longer.

Examination of *Prasiola crispa* from other localities, and at different times, has resulted in the finding of only isolated examples of this false-branching. It seems that the conditions required to produce the pseudo-branches in abundance are only locally or occasionally realised, so that their production is perhaps to be looked upon as a somewhat abnormal phenomenon.

IV.—Sexual Reproduction of *Chlamydomonas variabilis*.

The gametes of this species of *Chlamydomonas* do not appear to have been hitherto observed, or at any rate described. Wille

[1] Freshw. Algæ in Nat. Hist. Report, Brit. Antarctic Exped., 1910, Bot. Pt. 1, 1917.

[2] Or these cells may have been killed by some parasite.

[3] Wille, N., Algolog. Notizen, XI. Über die Gattung Chlamydomonas, Nyt Mag. f. Naturv. XLI, 1903, pp. 109-162.

in his monograph of the genus says, under *Chloromonas* (*Chlamydomonas*) *variabilis*, "Gameten ? Zygote ?"

Chlamydomonas variabilis Dang. has been found by the writer several times in the Midlands, and was very abundant and produced numerous gametes in a small temporary pond in a meadow at Quinton, Birmingham, during February, 1918. The characters of the vegetative cells agreed very well with Wille's description of the species, the form being more or less cylindrical, with a small anterior wart, and the chloroplast a parietal band not quite extending either to the posterior or to the anterior extremities of the cell, so that a small hyaline space was left at both ends of the cell. No pyrenoid was present, but numerous minute starch grains were scattered throughout the chloroplast. The stigma was in the posterior third of the cell. The plane of the first division of the cell was exactly transverse.

The first specimen taken from the pond showed that numerous gametes, many in process of fusion, were being produced (Fig. 2, E). The gametes are isogamous and much smaller in size than the vegetative cells. Size of gametes 8—10μ by 4·5—5μ (the vegetative cells were 15—22μ by 8—10μ).

Morphologically the gametes resemble the vegetative cells, except that the stigma is located nearer the middle of the cell. They have no cellulose wall, being clothed only with a very thin protoplasmic membrane. Eight gametes are produced by each mother-cell. Fusion commences at the anterior ends of the two gametes and gradually extends posteriorly (Fig. 2, F, G.) Partially fused pairs of gametes are still actively motile, and even when completely fused, so long as the cilia are retained, the zygote (zygozoospore) is still motile. The four cilia of each zygote, however, are soon lost and a thin cell-wall secreted (Fig. 2, H). The two stigmas persist for quite a long time in the walled zygospore, but, as the contents of the latter become more granular, they gradually disappear.

Zygospores were produced in hundreds and settled on the bottom of the wide-mouthed glass-jar into which the Alga had been placed. Some weeks after being formed numerous oil-globules appeared in the zygospores, the starch-grains gradually disappearing. The zygospore-wall remained smooth and colourless, and of moderate thickness. Width of mature zygospore 9—12μ. Their germination has not been observed.

PLANT FAMILIES: A PLEA FOR AN INTERNATIONAL SEQUENCE.

By Alfred Gundersen.

An almost endless variety of systems and modifications of systems of plant classification have been proposed. While the growth of knowledge demands constant revision, more urgent practical purposes require stability. The formation of a natural classification has become the task of morphology and paleobotany, almost entirely separate from systematic botany. The ideal system of the future must exhibit the course of plant evolution, but the establishment of this exact course is distant. Must meanwhile the confusion from a multiplicity of systems continue indefinitely?

Some Recent Systems.

The Engler-Gilg classification (1912) of the higher plant is:

EMBRYOPHYTA ASIPHONOGAMA.

1. Bryophyta.

2. Pteridophyta (Filicales, *Sphenophyllales*, Equisetales, Lycopodiales, Psilotales, Isoetales, *Cycadofilices*).

EMBRYOPHYTA SIPHONOGAMA.

1. Gymnospermæ (*Cordaitales*, *Bennettitales*, Cycadales, Ginkgoales, Coniferæ, Gnetales).

2. Angiospermæ (Monocotyledoneæ, Dicotyledonæ).

The apparently distinct line separating clubmosses and horsetails on the one hand (Lycopsida) from ferns and seed plants on the other (Pteropsida) was pointed out by Jeffrey in 1898. Scott (1909) considers the construction of the pedigree of the vegetable kingdom to be a pious desire, which will certainly not be realized in our time. To Jeffrey's groups he adds Sphenopsida, thus:

SPHENOPSIDA (Equisetales, *Pseudoborniales*, *Sphenophyllales*, Psilotales).

LYCOPSIDA (Lycopodiales).

PTEROPSIDA (Filicales, *Pteridospermæ*, Gymnospermæ, Angiospermæ).

Bessey (1914) adopts six main groups of vascular plants:

PTERIDOPHYTA (Eusporangiatæ, Leptosporangiatæ).

CALAMOPHYTA (*Sphenophyllineæ*, Equisetineæ, *Calamarineæ*).

LEPIDOPHYTA (Lycopodineæ, *Lepidodendrineæ*).

CYCADOPHYTA (*Pteridospermæ*, Cycadineæ, *Bennettineæ*, *Cordaitineæ*).

STROBILOPHYTA (Pinoideæ).

ANTHOPHYTA (Alternifoliæ, Oppositifoliæ).

According to Berry (1917) the practice of considering Angiosperms and Gymnosperms as sub-classes of the class Exogens was a no more pernicious mask of their true relations than the current usage which separates vascular plants into Pteridophyta and Spermophyta. He proposes seven groups : Angiospermophyta, Coniferophyta, Cycadophyta, Pteridospermophyta, Lepidophyta, Arthrophyta and Pteridophyta.

Conard recently (1919) urges that it is no longer possible to discuss the relationships of plants in the terminology of currently accepted classification, that systematic botany is in immediate need of revision along major lines, and proposes a dichotomous arrangement :

- THALLOPHYTA.
- EMBRYOPHYTA.
  - ATRACHEATA or Bryophyta.
  - TRACHEATA or Vasculares.
    - Lycopsida.
    - Pteropsida (Aspermæ or Ferns, Gymnospermæ and Angiospermæ).

UNIFORM FAMILIES BY AGREEMENT.

Slightly varying interpretations of the significance of characters, with corresponding variation in nomenclature, makes otherwise similar systems appear very different. In the past names now forgotten such as Phanerocotyledons, Acramphibrya, Rhizogens were given with a view to correspondence with other groups supposed to be co-ordinate. Agreement as to such main groups, even if obtainable, would have no important significance. Smaller groups have had a much greater stability. Ranunculaceæ, Papaveraceæ and numerous other family names are more than a century old.

The number of families of vascular plants is generally considered as about 300. For a number no greater, might not agreement be possible, agreement for a given period not only as to scope but as to sequence ? A family sequence, as compared with a complete system of classification would have practical advantages. First, being as to many questions *colorless* it would be more suitable for wide agreement, for the main groups may be variously named and arranged without affecting family sequence. Second, *revision* would mean mainly a rearrangement of sequence without the introduction of new names. Thus successive lists might have a considerable degree of continuity.

"Zoological and botanical systems," says a recent historian of biology, Miall, "owe comparatively little to individual lawgivers; they have been built up piecemeal by the incessant proposal of amendments, and the retention of such as proved satisfactory in practice . . . . . the discoveries, even of great men, have often been vitiated by serious mistakes, which have subsequently been corrected by men of far inferior power." The systems of the future, it seems inevitable, must more and more represent a general botanical synthesis rather than personal views.

Effective international agreements have been reached in a number of sciences. The confusion due to differing opinions as to the atomic weights of the elements was remedied by the establishment of an international list, in this case issued annually. It is of special interest that there is one list only, not many conflicting ones, and that it *bears the name of no individual or institution.* In astronomy the completion of the great international map of the sky depended on many agreements, in particular on a method of *dividing* the subject along definite lines recognized by all. Slightly varying systems of co-ordinates would have rendered international co-operation impossible.

Numbers as Part of Symbols for Families.

Whatever form of classification be used, many publications in all parts of the world require some *linear* sequence of families. A linear sequence is expressed by numbers. Was not the persistence of the Linnaean system in part due to its numerical clearness? "My system is but a tread of Ariadne," said Linnaeus, "a natural system is the first and last aim of systematic botany." Numbers are generally used in arranging genera and species. Dalla-Torre and Harms numbered genera have served in the arrangement of great herbaria. Numbered families have also been used in many publications and might have much wider uses. The somewhat complicated arrangement of the *Natürliche Pflanzenfamilien* into *Abteilungen* and *Teile* was much simplified in the *Pflanzenreich* by the adoption of family numbers assigned in advance, from IV-1 *Cycadaceæ* to IV-280 *Compositæ*. In Forbes and Hemsley's Index Floræ Sinensis family numbers are given *on every page*.

In the International Scientific Catalogue titles are classified by a system of numbers printed near the margin. These numbers at the same time *co-ordinate* the successive volumes. Thus articles on Gymnosperms are found by marginal number 6500 in any

volume. The precise assignment of these numbers is a matter of secondary importance in comparison with the advantages which come from their use.

Standard family numbers if established as a result of general consideration, thus dividing the world of plants along definite lines easily designated, might have various uses, for example :—

(*a*) They would be likely to give direction to morphological investigations.

(*b*) If lists of plants growing in many different parts of the world had the degree of unity implied by uniform family numbers, they would to a much greater degree than at present form a part of one work: the flora of the earth. Such lists would tend towards greater uniformity of nomenclature.

(*c*) Perhaps the time is yet distant when descriptive floras throughout the world may be arranged by a single system. Should it come the solution of numerous questions as to characters and distribution could not but be facilitated.

(*d*) Seed lists of botanic gardens, issued annually, are now arranged by a dozen different methods. Uniformity even among a few gardens would simplify exchanges and would naturally lead to increased co-operation.

(*e*) Botanical gardens cannot cultivate all plants, but wish to know: what are the plants of the world of greatest horticultural, economic or scientific interest? Uniformly arranged planting lists would tend in the direction of an answer, simplifying the work and increasing the value of collections.

(*f*) In the arrangement of numerous herbaria and other collections, especially smaller ones, such as those connected with instruction, where it is desirable that the arrangement should not be too distant from current views.

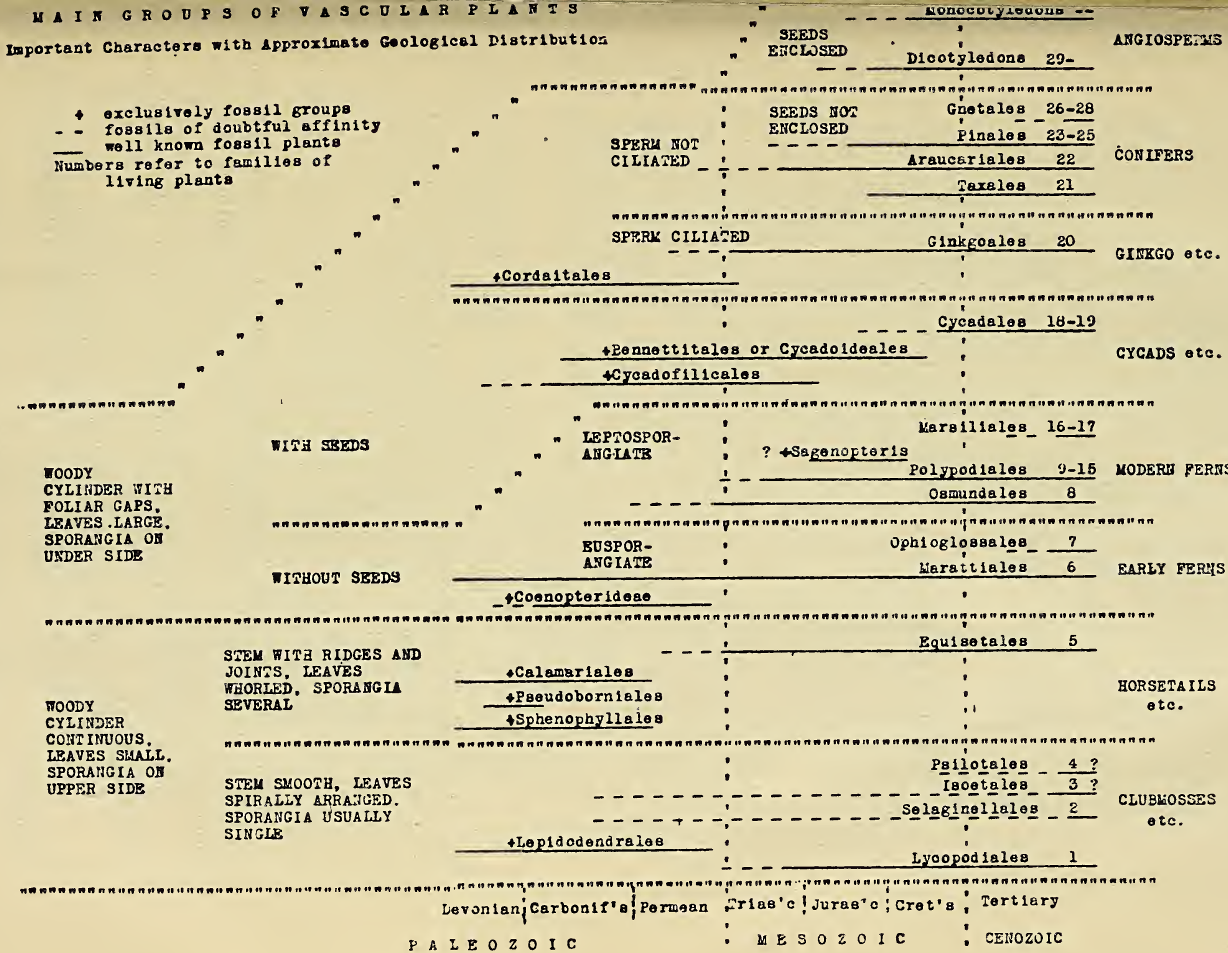
If after a period of years, preferably longer than ten, a different set of numbers should be adopted, this would only very slightly interfere with their benefits. Possibly alternate lists might make needed changes by inserted letters a, b, c as has been done by Engler. In any case hardly more than a pamphlet would be required to refer from the ten or twelve thousand genera of vascular plants as ordinarily used directly to family numbers, accompanied by abbreviated family names. The inclusion of genera in an index would not need to imply any recognition of the names. However, at some future time uniform families might naturally lead to an extension of the principle of *genera conservanda.*

An Inventory of Families.

If the desirability of uniform families should be approved by a number of botanists, or if possible by botanical institutions and societies in different countries, something like an inventory of facts and of conflicting opinions which appear to have a bearing on family sequence might be practicable. Such an undertaking would probably clarify many points, whether or not it should result in any world agreement. This would by no means require a re-writing of the *Pflanzenfamilien.* Details of genera and species, except in the cases where these affect the position of a family, would only confuse the issue. Evolutionary sequence is associated with more or less uncertain interpretation of characters; these characters are in nearly all cases very different from those by which plants are identified. Thus limited a survey might be completed within reasonable time. A single volume with a preliminary sequence, indicating the various possible arrangements, might contain more information than great works which include miscellaneous subjects.

The sequence adopted for the diagram on the opposite page is intended to call attention to some of the specific questions involved. The geologic distribution must be considered as only approximate. There are four main changes from the *Pflanzenfamilien* 1^0 *Lycopodiaceæ* etc. are not interposed between the ferns and seed plants; 2^0 ferns begin with eusporangiate forms as shown by Bower; 3^0 the ancient and diversified group of gymnosperms requires a greater number of families, as used by many authors; 4^0 angiosperms begin with dicotyledons. The families might then begin somewhat as follows:

Lycopodiaceæ	Lycop	1	*Sagenopteris*		
Lepidodendrales			Marsiliaceæ	Mars	16
Selaginellaceæ	Selag	2	Salviniaceæ	Salv	17
Isoetaceæ	Isoet	3			
Psilotaceæ	Psil	4 ?	*Pteridospermæ*		
			Cycadaceæ	Cycad	18
Sphenophyllales			Zamiaceæ	Zami	19
Pseudoborniales			*Bennettitales*		
Calamariales					
Equisetaceæ	Equis		*Cordaitales*		
			Ginkgoaceæ	Ginkg	20
Coenopterideæ					
Psaronieæ.			Taxaceæ	Taxac	21


MAIN GROUPS OF VASCULAR PLANTS
Important Characters with Approximate Geological Distribution
+ exclusively fossil groups
- - fossils of doubtful affinity
—— well known fossil plants
Numbers refer to families of living plants
SEEDS ENCLOSED
Monocotyledons
Dicotyledons 29-
ANGIOSPERMS
SPERM NOT CILIATED
SEEDS NOT ENCLOSED
Gnetales 26-28
Pinales 23-25
Araucariales 22
Taxales 21
CONIFERS
SPERM CILIATED
Ginkgoales 20
GINKGO etc.
+Cordaitales
Cycadales 18-19
+Bennettitales or Cycadoideales
+Cycadofilicales
CYCADS etc.
WITH SEEDS
LEPTOSPORANGIATE
Marsiliales 16-17
? +Sagenopteris
Polypodiales 9-15
Osmundales 8
MODERN FERNS
WOODY CYLINDER WITH FOLIAR GAPS, LEAVES LARGE, SPORANGIA ON UNDER SIDE
EUSPORANGIATE
Ophioglossales 7
Marattiales 6
EARLY FERNS
WITHOUT SEEDS
+Coenopterideae
Equisetales 5
STEM WITH RIDGES AND JOINTS, LEAVES WHORLED, SPORANGIA SEVERAL
+Calamariales
+Pseudoborniales
+Sphenophyllales
HORSETAILS etc.
WOODY CYLINDER CONTINUOUS, LEAVES SMALL, SPORANGIA ON UPPER SIDE
Psilotales 4 ?
Isoetales 3 ?
Selaginellales 2
CLUBMOSSES etc.
STEM SMOOTH, LEAVES SPIRALLY ARRANGED, SPORANGIA USUALLY SINGLE
+Lepidodendrales
Lycopodiales 1
Devonian Carbonif's Permean Trias'c Juras'c Cret's Tertiary
PALEOZOIC
MESOZOIC
CENOZOIC

Marattiaceæ	Marat 9	Araucariaceæ	Arauc 22
Ophioglossaceæ	Ophio 7	Pinaceæ	Pinac 23
		Taxodiaceæ.	Taxod 24?
Osmundaceæ	Osmun 8	Cupressaceæ	Cnpr 25
Gleicheniaceæ	Gieich 9	Ephedraceæ	Ephed 26
Matoniaceæ	Maton 10	Welwitschiaceæ	Welw 27
Hymenophyllaceæ	Hymen 11	Gnetaceæ	Gnet 28
Schizæaceæ	Schiz 12		
Ceratopteridaceæ	Cerat 29	DICOTYLEDONS 29—	
Cyatheaceæ	Cyath 14		
Polypodiaceæ		MONOCOTYLEDONS.	

Seeking a maximum of stability it is not desirable to assign numbers to exclusively fossil groups. For the same reason groups such as ferns or monocotyledons are not numbered separately; the position or delimitation of such groups may be different in the future. But with a single series as of vascular plants, possibly later extended to all plants, the numbers would be essentially *symbols*; periodic changes due to improved classifications would require practically no new names, only a reassignment of numbers. In the case of a few very large families, such as the Compositæ, it might be preferable that the numbers should refer to tribes. The thought is here of the co-ordination of information rather than of the arrangement of collections.

The angiosperms in the *Pflanzenfamilien* are arranged according to a rigid system of floral morphology. Among questions which would need to be considered in a possible rearrangement are:

(*a*). Whether woody plants should generally precede herbaceous ones within a given relationship;

(*b*). Whether at least apetalous herbaceous plants should follow related polypetalous ones;

(*c*). Whether *Piperales* should be removed from its position between *Casuarinaceæ* and *Salicaceæ* to a later position perhaps near *Polygonaceæ*;

(*d*). Whether *Proteaceæ* should be nearer the earliest angiosperms;

(*e*). Whether *Aizoaceæ* and *Cactaceæ* are related;

(*f*). Whether *Caryophyllaceæ*, *Linaceæ* and *Gentianaceæ* are related;

(*g*). Whether *Cornaceæ* should be near *Caprifoliaceæ*;

(*h*). Whether *Cucurbitaceæ* should be near *Passifloraceæ*;

(*i*). Whether groups such as *Mimoseæ*, *Clusieæ*, *Cichorieæ* etc. should be considered as families;

(*j*). Whether *Alismaceæ* are the primitive monocotyledons;

(*k*). What are the relationships of the *Palmæ*;

(*l*). Whether *Araceæ* are related to *Piperaceæ*.

SUMMARY.

The present article may be briefly summarized:

1. A periodic inventory of facts and opinions which appear to have a bearing on the sequence of families, especially of living vascular plants, is greatly to be desired.

2. Where facts are not conclusive the definite goal of a truly international sequence should be sought through agreement.

3. Standard numbers as part of symbols for plant families, revised at suitable intervals, would serve important practical purposes, especially in the co-ordination of information.

In conclusion it may be said that if it should be widely agreed that an international family sequence were desirable, ways would doubtless be found to overcome the various difficulties in the way of its establishment. Discussion of the subject by those interested might be a first step.

BROOKLYN BOTANIC GARDEN.

REFERENCES.

Bancroft, N. Review of Literature Concerning the Evolution of Monocotyledons. *New Phytologist*, 13: 285-308, 1914. (With bibliography).

Berry, E. W. The Classification of Vascular Plants. Proc. Nat. Acad. Sci. 3: 330-333, Washington. 1917.

Bessey, C. E. The Phylogenetic Taxonomy of Flowering Plants. Annals Missouri Bot. Gar. 2: 109-164, 1914.

Bessey, E. A. The Origin of the Anthophyta. Michigan Acad. Sci., Ann. Report 17: 142-151, 1915. (With bibliography).

Bower, F. O. The Origin of a Land Flora. London, 1908.

Conard, H. S. The Classification of Vascular Plants: A Review. Plant World 22: 59-70, 1919. (With bibliography).

Engler, A. & Gilg, E. Syllabus der Pflanzenfamilien. Berlin, 1912.

Jeffrey, E. C. The Anatomy of Woody Plants. Chicago, 1917.

Warming, E. Fröplanterne. Copenhagen, 1912.

Wernham, H. F. Floral Evolution. *New Phytologist*, 10: 74, 109, 145, 217, 293; & 11: 145, 217, 290, 373; 1911-1912.

THE EVOLUTION OF PRIMITIVE PLANTS FROM THE GEOLOGIST'S VIEWPOINT.

BY CHARLES SCHUCHERT.

THE writer has read with a great deal of profit A. H. Church's recent valuable memoir, "Thalassiophyta and the Subaerial Transmigration"[1] and A.G.T.'s clear and searching review of it, "The Evolution of Plants."[2] Church's paper is of great importance not only to all botanists, but to all teachers of Historical Geology as well, and the writer, as a member of the latter group, is thankful to him for having written it. As paleontologists we may accept his conclusions and leave to the botanists the discussion as to the course of evolution the marine algæ took in their ascent to land plants. As a paleontologist and geologist, however, the writer cannot accept some of Church's geologic dicta, and since the editor of the NEW PHYTOLOGIST invites criticism, the following questions may be raised.

First, did the earth ever have a universal ocean? Second, has the amount of water in the hydrosphere decreased or increased during the geological ages? Third, was the primal ocean as salty as it is to-day, and what is the source of these salts?

The answers to these questions must be sought in the light of what is going on in the world about us and of what the astronomers, geophysicists, and geologists tell us about the evolution of the galaxy and of the constellation of the sun, and the origin of the earth. The famous Laplacian theory of earth origin, adapted by the elder Dana to the earliest stages of earth evolution, is now badly shattered, and out of it has risen a new one, the Chamberlin-Moulton planetesimal hypothesis. In accordance with this later theory, the earth never was a star that finally became encrusted with a rocky surface, above which floated an atmosphere holding all the water now on the earth's exterior and that which has percolated to the exterior portion of the lithosphere during the geologic ages. The universal ocean of the ancients, fastened upon geology more than a century ago by Werner, was a figment of his imagination. On the contrary, the earth's oldest surface, probably never to be discovered, was composed of far more dry land than water. Ocean basins in the sense of those of to-day may then not have existed. All of the water on the face of the earth has been

[1] *Oxford Botanical Memoirs* **3,** 1919. Oxford Univ. Press. Price 3s. 6d.

[2] NEW PHYT. **19,** 1920, p. 1.

slowly liberated by the earth itself, as "juvenile water," through its volcanoes and thermal springs. What we see to-day of vadose (=old) waters is the accumulation of more than one thousand million years. Likewise the salts of the seas and oceans have been of slow gathering, for they have been gradually washed out of the land and have accumulated in the oceanic basins during the great length of geologic time. The rivers of to-day are known to be variably saline, and it is their small daily additions to the seas that have gone towards making up the vast amounts of salts contained in the latter, locked up in the rocks as rock-salt, or forming part of the enormous limestone and dolomite beds of the geologic formations. This subject is treated in detail in Chamberlin and Salisbury's "Geology" or in shorter and more popular form in "The Evolution of the Earth and its Inhabitants," a series of papers by Yale instructors.

We now know that the oceans did not always remain within their confines as at present delimited, for the many well known fossiliferous deposits on the continents attest that the marine waters have been over the latter. Since the beginning of the Paleozoic, the oceans have repeatedly flooded the lands more or less widely, but never have all the lands of any one time been beneath the seas. What has been true since the Cambrian was probably equally so for Archeozoic and Proterozoic times; but with this difference, that the water basins and the continental protuberances in the Archeozoic were probably smaller and by far greater in number than they are to-day.

What is the bearing of these statements on Church's theory? Certainly they do not disprove his conclusions, rather do they appear to make all the more easy the solutions along his lines of thinking. We may therefore agree with him that nearly all life in the earliest Archeozoic consisted of oceanic micro-plankton, but that the oceans did not then have their present depth and that there were lands with shores and shallow-to-littoral seas, with sunlit bottoms, just as there are to-day. Accordingly some of the plankton, after it had evolved into nucleated cells living in colonial form, might easily have found a bottom where assimilation could have been continued, though probably more slowly than in the surface waters. With the finding of this favorable bottom for the continuance of life, a new factor in organic environment was introduced, and out of the struggle for adaptation to it there arose the plant benthos.

We know that a far greater variety of life is found in the salty waters of the seas and oceans than is the case in the fresh waters of the present and the past. The many kinds of salts in the oceans appear to be a stimulus toward individual and specific differentiation. To-day the marine waters have about 3·5 per cent of salts and three quarters of these are sodium chloride. This present quantity, however, is, as has been said, the accumulation of the geologic ages, and from this conclusion it follows that the Archeozoic oceans had far less salts and probably a different salt combination. It is likely that at all times the oceans were salty, but in late Archeozoic time the amount may not have risen to one half what it is now. The lime and magnesium salts in solution may have been at first far greater in quantity than at present, but as soon as denitrifying bacteria came into existence, the warm water oceans were probably freed of their lime sulphates as quickly and as thoroughly as they are at present. It would also appear that the oceans originally received far less nitrogen from the lands than they do now, since the continents of Archeozoic time had no land plants to assist in taking this element out of the atmosphere and in turn furnishing it to the rivers to transport to the seas.

Church is very positive that the primitive lands could have had no soils and that everywhere there was a hard rock surface until they were clad with verdure. But an earth with an atmosphere holding water vapor was bound at once to break down the rocks and so to form soils. The sediments of the Archeozoic formations were derived from crystalline rocks, the original source of all sedimentary strata. Their nature is like that of the Proterozoic sediments, and since these latter are far less metamorphosed, it can be definitely stated that a study of them leads to the conclusion that the lands must have had, ever since there was an atmosphere and rain, arkoses (broken up crystalline rocks without chemical alteration) and soils, for if not, whence came the marine sediments? Of course these primitive soils had no humus in them, for there was no land life from which this could be made, but we can depend upon it that along the seashore and in the marine swamps the detritus of the land was most comminuted and also more or less changed chemically. Here the waves would wash out, and the wind distribute, some of the moribund life of oceans, and therefore land humus had its origin at the sea margin. With the adaptation of the hardier marine seaweeds to these marginal strips of shore, the *transmigration* of the plants of the oceans over the lands was begun.

A far more favourable condition for this transmigration is to be sought in the variable nature of the sea-level, due to crustal movement. We know that during the Paleozoic the oceans invaded North America at different times to the extent of millions of square miles. These overfloodings were shallow seas—epeiric seas—with an average depth of probably less than 500 feet. Now think of these seas withdrawing very slowly from the land, and see what a favorable ground for humus must have been left in their wake, where the seaweeds might become adapted to the new environment that was thus forced upon them. Just as the fishes had to develop legs and lungs if they were to become the land-living amphibia of the Silurian or Devonian, so the Thalassiophyta, probably as early as the Archeozoic, were forced to become Xerophyta.

YALE UNIVERSITY.

PRELIMINARY NOTE ON A HYDRION DIFFERENTIATION THEORY OF HELIOTROPISM.

BY JAMES SMALL, D.Sc.

FURTHER work, which is now proceeding on the influence of carbon dioxide on geotropism and heliotropism, having indicated that the carbon dioxide balance is, indeed, of the fundamental importance previously suggested (1, p. 51 and 2, p. 208), a hydrion differentiation theory of heliotropism has been developed As it will be some time before the experimental work now in progress can be completed, the theory has been considered of sufficient interest in itself to warrant a brief description.

It has been suggested, and there is more experimental evidence accumulating in support, that the direction of geotropic curvatures is governed by the hydrion concentration of the continuous phase of the plasma membranes of the perceptive cells. The present theory is that the same is true for heliotropic curvatures.

Briefly, it is suggested that light, either by increasing photosynthesis and the amount of respirable material or more probably

in some other way, increases the rate of respiration in the perceptive cells. This increase in respiration involves an increase in the carbon dioxide within the cells affected. Such an increase in carbon dioxide involves in "root" structures an increased hydrion concentration of the already relatively acid continuous phase of the plasma membranes, giving increased relative acidity with consequent increase in polarisation and in turgidity. Root structures, therefore become more turgid on the side which is more illuminated, and show negative heliotropism.

The increase in carbon dioxide within the perceptive cells in "stem" structures involves an increased hydrion concentration of the already relatively alkaline continuous phase of the plasma membranes, giving decreased relative alkalinity with consequent decrease in polarisation and in turgidity. Stem structures, therefore, become less turgid on the side which is more illuminated, and show positive heliotropism.

Since this explanation of heliotropism holds for non-chlorophyllous roots, fungi, sporogonium stalks (e.g., *Pellia*), etc., as well as for chlorophyllous structures, it is more probable that light reacts directly on the amount of respiratory carbon dioxide, rather than indirectly by increasing the amount of respirable material. This aspect, as well as others, is now receiving attention, and reversed curvatures both geotropic and heliotropic have been obtained in atmospheres containing a large percentage of carbon dioxide.

Botanical Department,
The Queen's University of Belfast.

October 28th, 1920.

1. Small, J. A Theory of Geotropism, New Phytologist, Vol. XIX., p. 49.
2. Small, J. and Rea, M. W. Preliminary Notes I. On the Reversal of Geotropic Curvature of the Stem. Ibid. Vol. XIX., p. 208.

REVIEW

"Fossil Plants. A Text Book for Students of Botany and Geology." By A. C. Seward. Vol. IV, Cambridge, 1919, pp. XVI and 543, Figs. 630—818.

THE fourth and last volume of Professor Seward's text book of palæobotany completes the account of the fossil Gymnosperms, including the Ginkgoales, Coniferales and Gnetales. The Ginkgoales, which formed a considerable element of many past floras, are fully treated, but they are known mainly by leaf impressions, the abundance of which makes it surprising that so little is known of other parts of the plant. There are scarcely even any reliable records of fossil Ginkgoalian wood. A short chapter at the end of the book is sufficient for supposed fossil examples of the Gnetales, none being of any great botanical importance, and the main part of the book is devoted to the Coniferales, introduced by a very valuable and well-illustrated chapter on recent conifers.

In dealing with fossil forms, the foliage shoots and reproductive organs, though often difficult to correlate, are described together by Professor Seward as far as possible under each family, with an additional chapter for wholly doubtful genera, while the wood is given separate treatment. This arrangement is undoubtedly the best in the present state of palæobotanical knowledge, which makes it very difficult to get a connected idea of the plant as a whole, a difficulty which is reflected in the nomenclature used by palæobotanists, necessitating the use of provisional "generic rubbish-heaps" such as *Brachyphyllum* and *Pagiophyllum*, and the multiplication of "genera" for different organs of what may be the same plant. The use of the same name for sterile branches and for unconnected cones has in the past added considerably to the confusion, and the present exhaustive work has reduced to something like order the terminological chaos which enveloped the numerous fossil impressions of twigs, leaves and cones, and will considerably lighten the task of all future workers.

The classification of fossil coniferous woods as revised by Gothan is accepted with some modifications by Professor Seward, who thinks that Gothan has carried generic subdivision too far. For example, he substitutes a new name, *Mesembrioxylon*, for the two genera *Podocarpoxylon* and *Phyllocladoxylon*. These two groups are certainly very difficult to distinguish, even when the preservation is perfect, and it is perhaps best for the present not to attempt to separate them, but Professor Seward's view of the implications of the names would probably not be admitted by Dr. Gothan. Speaking of *Podocarpoxylon* and *Phyllocladoxylon* (p. 203) he says "the use of Gothan's names implies affinities to recent genera which there are no adequate reasons for assuming," yet on another occasion he himself states that "the fossil wood described under *Cedroxylon* does not denote that the parent plants were more closely allied to *Cedrus* than to some other genera of the same family" (p. 369), which seems to be the most satisfactory view to take of all such names. And if fossil woods have been too

minutely subdivided, there seems no very strong reason for retaining such a genus as *Planoxylon*, which has no characters by which it may be distinguished from *Protocedroxylon*, a name accepted by Professor Seward without comment, though Dr. Stopes considers that it is objectionable on the ground of unfounded implications of affinity.

A consideration of the evidence so carefully brought together and arranged by Professor Seward shows that we are not yet in a position to give conclusive answers to the many interesting problems connected with the phylogeny of the Coniferales. While stating that the group is probably monophyletic, Professor Seward refrains from giving any decisive opinion as to the stock from which it sprang. He thinks that the weight of evidence is in favour of the Araucarineæ being older than the Abietineæ, but that at present we can say little more definite than that the latter had a later maximum development than the former. The evidence from foliage shoots and cones is somewhat uncertain, but the fossil wood points to the Araucarineæ as being older, though Cordaitean and Arancarian woods have not yet been satisfactorily separated. Professor Seward is very cautious about most supposed pre-Jurassic Araucarians, though he thinks that many forms (*e.g.* of *Walchia*, *Voltzia* and *Ullmannia*) show undoubted Araucarian affinities. He concludes that the *Araucaria* type is older than that of *Agathis* (*Araucarites Delafondi* from the Permian is one of the earliest definite examples of an araucarian cone-scale), and points out that this once cosmopolitan family continued to flourish in the northern hemisphere till well into the Tertiary period.

It is unfortunate that the Podocarpineæ, which may be allied to the Araucarians, are very unsatisfactorily represented in the geological sequence, and records of undoubted Taxineæ are also very rare. The Cupressineæ and Abietineæ were abundant in later Mesozoic times, though correlation with living genera is difficult, and there are many fossil forms which cannot even be placed with certainty in any particular family. It is to be hoped, as Professor Seward suggests, that the cuticular study of these impressions will be of some help in classification, for little has been done in this direction so far.

In conclusion, one may say that this volume marks a definite stage in our knowledge of the past history of the conifers, and it indicates clearly the gaps which must be filled in by future investigation. It is a matter for regret that the fossil Angiosperms are not yet ripe for similar treatment, and that this important work is now concluded, but all botanists will look forward eagerly to Professor Seward's promised general survey of past floras, which could not be included in a descriptive text book.

W. N. E.

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THE
NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL

EDITED BY

A. G. TANSLEY, M.A., F.R.S.
UNIVERSITY LECTURER IN BOTANY
CAMBRIDGE

IN CONSULTATION WITH THE STAFF OF
THE CAMBRIDGE BOTANY SCHOOL

VOLUME XX

PAGES VIII AND 248

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INDEX OF SUBJECTS

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Vol. XX, No. 1 March 24th, 1921

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THE

NEW PHYTOLOGIST

VOL. XX, NO. 1 MARCH 24, 1921

EDITORIAL

THE past three years have been an anxious time for those financially responsible for the publication of periodical scientific literature, and the anxiety is not yet removed. The costs of production have increased more than threefold from the pre-war level, continental subscriptions have not been renewed owing to the unfavourable or even prohibitive rates of exchange, and many home subscribers have been compelled to cease their subscriptions owing to the increased cost of living. These difficulties have been partly met by various economies, by raising prices and by reducing the bulk of matter, but such measures have limits beyond which they cannot be carried without defeating themselves. No journal can be permanently successful which does not present a reasonable amount of varied and attractive matter at a price which its readers can afford.

The moment therefore seems opportune for an appeal to contributors to do their part in helping to carry out these objects, since it is to the interest of contributors and readers alike that a scientific journal should contain as much varied matter in as short a space as is practicable, and should have as large a circulation as possible.

The two points to which attention should particularly be directed are these:

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THE BIOCHEMISTRY OF CARBOHYDRATE PRODUCTION IN THE HIGHER PLANTS FROM THE POINT OF VIEW OF SYSTEMATIC RELATIONSHIP

A CONTRIBUTION TO THE DISCUSSION ON BIOCHEMICAL CLASSIFICATION OF PLANTS AT THE CARDIFF MEETING OF THE BRITISH ASSOCIATION

By F. F. BLACKMAN

In surveying the Carbohydrate Economy of Flowering Plants as a whole, we note that there is a general uniformity, interspersed with some strikingly aberrant cases. These exceptional cases are not distributed indiscriminately, but tend to characterize groups of plants which are classed as related systematically, which we interpret in terms of common phyletic origin. The attempt of the present contribution is to review some of these biochemical diversities of carbohydrate production and see what they look like as steps toward a biochemical classification of plants, and how they rank with the morphological characters on which groups of flowering plants have been mostly drawn up.

Carbohydrate production can be analysed into three strata, representing progressive stages of what we may call the up-grade carbohydrate flux.

We have (1) the primary photo-reduction of carbonic acid involving light-energy and specific pigments: (2) the immediate appearance of sugars; which seems to be universal: (3) the subsequent appearance, though by no means universally, of complex polysaccharides, which are deposited in the chloroplasts. Similar bodies are also formed in the leucoplasts of storage organs from sugars arriving from the leaf by translocation.

These three stages represent increasing chemical condensation to larger and larger aggregates. The first stage, derived from reduction

of carbonic acid may be assumed to be, initially, a molecule with one carbon atom. Formaldehyde is the substance that satisfies all theoretical considerations, though its actual occurrence has not been proved. For the second stage we jump to sugars with 5 and 6 carbon atoms, pentoses and hexoses, while from the latter by doubling we get 12-carbon sugars, of which cane-sugar is the most obvious. For the third stage we have much condensed polysaccharides like starch, inulin, etc., in which the number of carbon atoms may run up to several hundreds.

Now as we are making bold to consider the biochemical vagaries of protoplasm with a critical detachment, we may ask why these stages occur and not others, why the plant revels in the hexoses, makes a certain play with pentoses but does next to no traffic in sugars of 3, 4, 7 or 8 carbon atoms—the trioses, tetroses, heptoses, and octoses, all of which are preparable in the laboratory. The hexose, glucose, is undoubtedly the key-sugar to carbon-metabolism whether we consider up-grade processes or down-grade ones like respiration and fermentation. Considered purely chemically, glucose is a molecule of remarkable properties, combining a certain stability in pure solution with an extraordinary potentiality of varied chemical change in presence of what the pure chemist might call impurities. Now biochemistry is not the chemistry of pure substances but the chemistry of impure substances, indeed of very impure substances. It is a mild suggestion that always in the cell, several dozen impurities are present with any one substance that we concentrate attention upon.

In considering the important *rôle* that various sugars play, the biologist sometimes drifts into the teleological way of thinking, and regards the cell as having selected these sugars as specially suitable for its purposes.

Let us turn then to the test-tube for illumination on this matter, and particularly to the wisdom drawn from the test-tube by Nef in his elaborate researches on what we may call the purely chemical metabolism of sugar molecules. Nef, at Chicago, up to his recent death, devoted some fifteen years to studying the spontaneous chemical changes undergone by sugars in the presence of impurities, such as salts and hydrates of sodium and other metals. He showed how every single sugar, be it of 1, 2, 3, 4, 5 or 6 carbon atoms, tends to pass over into all the others, so that an equilibrium mixture of more than a hundred derivatives may arise in the course of weeks

by spontaneous interactions. All this radiating flux represents the purely chemical background of possibilities out of which the cell forms its particular uni-directional stream-lines of metabolic flux. What we have to investigate in protoplasm is the mechanism that determines change in one direction rather than others, out of the chemically limited possibilities.

To return to the fact that hexoses and pentoses occupy the first and second place in carbohydrate metabolism to the exclusion of the adjoining classes of tetroses and heptoses. Nef has shown that this is inherent in the structure of the different sugar molecules themselves. When formaldehyde is condensed by lead hydrate *in vitro* it is found that the end-products are almost entirely derivatives of just these two classes of sugars. Lower sugar-classes have merely a transient existence as intermediate stages in the test-tube—as in the cell; and in neither does condensation go on to higher classes of sugars such as heptoses.

We get real light on the cell and its possibilities and limitations from his general conclusion that just those individual hexoses which are abundant in plants, are exactly the ones whose derivatives tend to accumulate in the test-tube, having a certain inherent degree of stability. Nef's picture leads us on further, to imagining traces of innumerable sugar derivatives and forerunners present in the cell, as transitional states. Research directed towards more complete identification of cell-activity with purely chemical activity *in vitro*, on these lines, is very difficult and hardly begun yet. Up to the present we have had to be content with identifying only those substances which occur in bulk in the cell.

Understanding now why hexoses are so abundant in carbohydrate economy, our attention may next be turned to pentoses.

The drift of recent opinion is towards believing that pentoses really play a more important part in the cell than has hitherto been recognized. Pentoses, and their particular polysaccharides, pentosans, are important constituents of the nucleus, of certain cell-walls, and of mucilage, but little general metabolic significance has been allowed them.

Now, in a particular type of plant, pentoses and pentosans are abundant. Spoehr in his work on the carbohydrate economy of Cacti has emphasized their importance in relation to plants that exhibit the type of structure and physiology that is known as 'succulent.' Recently a remarkable pronouncement has been made on the real factor which determines the succulent habit, which habit

had before been attributed to the water-relations of succulent plants to the arid soils in which they grew. In this paper on 'The Basis of Succulence' three Americans, MacDougal, Richards and Spoehr, who have worked more or less independently on succulents, have come to the agreed conclusion that succulence is due to a "metabolic complex favourable to pentose formation." Pentoses lead on, by condensation, to pentosan-mucilage with special water-holding properties, and to other characteristics so marked in succulents.

We may accept it then that here we have a deep-seated aberration of the ordinary carbohydrate flux tending more to the production of pentoses than usual. Here is one of those biochemical variations that we spoke of in opening, and it becomes of interest to note the distribution of succulence among flowering plants. Certain families of plants are characteristically succulent, such as Cactaceae and Crassulaceae, but we find succulent genera and groups of genera here and there among other families. *Rochea,* among the Compositae is a well-known example of an isolated succulent genus, but it possesses all the correlated physiological and anatomical properties that are found in the typical succulent families.

It would seem that we must assume that the mutation in protoplasmic constitution, which determines this direction of carbohydrate-flux, has occurred a number of times independently and that in some cases this has been followed by evolution of a whole group of allied genera and species, retaining the character, while in other cases only a single isolated form perpetuates the mutation.

After this example let us turn to a biochemical point in which there is great variation through the range of flowering plants. This concerns the transition from the second stage, that of sugars, to the third stage, that of polysaccharides. It is well known that a number of plants form starch freely in their chloroplasts, as a so-called 'temporary reserve' of the carbohydrate produced by photosynthesis, while many plants, on the other hand, form little or none. Mayer, in 1885, investigated all the plants in a botanic garden from this point of view and he found that this characteristic mostly holds true throughout a family of plants. He grouped the families examined into five classes, running from those that form starch very richly —Class I—to those that form none at all—Class V. Among Dicotyledonous families, most come in Class II, Solanaceae and Papilionaceae being alone in Class I, while Class V is represented only by Gentianaceae. When we come to Monocotyledonous families, it is

striking to find no family worthy to come in Class I or Class II, while most of them come at the tail in Classes IV and V. Here we seem to have a definite shifting of a biochemical character, possibly early in the separation of the two morphological types. Isolated exceptions occur to this general relation, as for example, *Hydrocharis* among the Monocotyledons which condenses its sugar to starch in great abundance. Both types of leaf, the starch-leaf and the sugar-leaf, seem to be quite adequate, physiologically, and neither suggests any real biological advantage over the other.

This sugar-leaf and starch-leaf distinction can, however, be analysed a stage deeper, so that we believe we know what it turns upon. It is not due to any lack, in Monocotyledons, of the agent which determines the condensation of sugar to starch, but to the high critical concentration of sugar that is needed to start starch-formation. If sugar can be got into the cells in sufficient concentration, then starch is visibly formed in leaves of the sugar-leaf type also. This can be done quite simply by floating cut pieces of leaf upon strong enough sugar solution in the dark. In 1898 Winkler showed that with ordinary starch-leaves, 0·2 to 0·5 per cent. sugar is the critical concentration. The moss *Mnium* gives the lowest value of 0·05 per cent. For sugar-leaves we have values like 15 per cent., while the leaves of the sugar-cane are found to require 18 per cent. sugar. Only one plant has such a high value that it has resisted all attempts to force it into starch-formation, and that is the Onion, which can be got to store nothing but sugar however it is treated.

This 'critical concentration' theory is supported by all workers on the subject. It indicates that there is not a simple equilibrium-relation between starch and sugar; and that, as Lundegardh has urged, starch-formation is a complex happening still requiring a good deal of quantitative investigation. One of the fascinating points of departure from simple chemical expectation is, that cane-sugar is a better sugar for artificial starch-formation than either maltose or glucose.

We judge then that Monocotyledons are characterized by a high critical sugar-concentration generally, while Dicotyledons show a low one. This distinction seems to be merely one of degree and not of kind, so that it is hard to say to what sharply defined protoplasmic character it may be attributed. The distribution of this character over families is quite like that of succulence, showing here a wide sweep over a large number of related genera and there an isolated example.

These biochemical characteristics, then, in the matter of their scatter, remind one of those morphological characteristics which are of secondary or tertiary importance rather than of the fundamental distinctions which hold without exceptions for large aggregates of families.

For a last point we may take up the fundamental problem of whether a biochemical classification of plants is conceivably attainable, given enormously increased knowledge. Assuming that all morphological as well as all metabolic features of plants must be the outcome of definable attributes of protoplasm, it seems clear that even if we could state these, we should still have the difficulty of balancing up conflicting affinities to decide phylogenetic relationship and that, as now, everything would turn upon consensus of evidence, before the biochemist could arrange his metabolic variants in families, genera, species and forms.

We may well assume that the protoplasm of every form differs from that of every other in some particulars and that these differences, at the minimum, might be those of a set of systems composed of optical isomers. The richness of protoplasmic systems in proteins and carbohydrates would make far more stereo-isomeric variants possible than there are different living species and forms. On this basis plants would be classified by the configuration of their protoplasmic atomic groupings in space, instead of by the configuration of their flowers and allied features. Ultramicroscopic form and morphology would replace macroscopic.

A thorough-going attempt has been made recently to explore plant-protoplasmic activity to see whether such a conception of innumerable different stereo-isomeric protoplasms corresponds to anything in the actual facts of biochemistry. This laborious work has been undertaken by Reichert and the Carnegie Institution.

After Reichert had shown that the haemoglobins of all animal-genera examined could be differentiated by crystallographic and other characters, so establishing a biochemical specificity of animal organisms, he decided to extend the same sort of enquiry into the plant kingdom.

The substance selected was starch. His underlying conception was that branches of the protoplasm in amyloplasts responsible for the condensation of starch would probably possess slight stereochemical differences from species to species and that this must determine corresponding differences in the arrangement in space of

the condensed hexose units. The lowest molecular weight for starch is 15,000, which indicates the condensation together of at least 90 hexose units and so suggests many more possible stereo-isomers than there are starch-bearing plants.

Reichert's first investigation, published in 1913, was directed to enquiring if the starch-grains of all species of plants are demonstrably different. For the 300 species examined the answer is in the affirmative. A few weeks ago there reached this country a second publication containing a minute study of the starch-grains of parents and crosses. These two investigations together fill four huge quarto volumes for which the Carnegie Institution has subsidized the publication of 800 photo-micrographs of starch-grains, 1100 graphic charts of their reactions, as well as some 1700 pages of text.

For each plant, the isolated starch-grains are examined for some twelve characteristics; four points of visible form, two of appearance in polarized light, two of staining with aniline dyes, several of reactions with iodine and other agents and finally the solution-temperature or rate at which the grains lose their solid form when heated with water, which temperature ranges from 49° to 90° Centigrade. No two of these characteristics seem to be closely correlated and Reichert treats them all as 'unit characters.'

Graphic charts are constructed by giving a numerical value to the degree of reaction of a given starch to each of these agents, so that the eye can take in, as a whole, all the different behaviours of each starch in the form of a curve. No great accuracy is claimed for the detailed values, as the whole work is entitled a preliminary exploration. The results certainly support the thesis that no two species or cultural forms have quite identical starches, and that in crosses the starches of the cross show a varying behaviour, but incline more towards the characters of the seed-parent.

From his review of genera and species, the author concludes that nearly always the starches of species of one genus resemble each other more than they resemble species of other genera. Genera, too, often show similarity within one family. Indeed, it is interesting to find how closely, on the whole, the starch-characters accord with the subdivisions of classification accepted for flowering plants. Starch-evidence has definite contributions to make to the doubtful relationships of certain genera, and indicates that some families are homogeneous and others heterogeneous.

No individual details are given as to the part of the plant the starch-grains were taken from, but the general statement is made

that, in all cases, it came from organs subserving vegetative reproduction. We should be glad to learn the characters of the starch-grains formed in the leaves of some of these plants for comparison. If all plastids arise from a common origin by division we should expect definite relations, on the present hypothesis, between the starch products of chloroplast and of leucoplast. As Reichert says, an enormous amount remains to be done, but the whole situation is full of suggestion and interest. There is however, as yet, no indication that the different starches are merely stereo-isomers. The researches of Max Samec show what a complex colloid one has in natural starch.

In conclusion, we may recall how differently the matter stands with the pigments of the chloroplasts from species to species. It is true that Étard in 1906 asserted that there were an enormously large number of different chlorophylls in different plants, but all this has disappeared before Willstätter's demonstration of the extraordinary uniformity of the chlorophyll pigments throughout the higher plants. Influenced by this identity of pigment, we imagine identity in the simple first product of photo-reduction of carbonic acid in all cases. From this initiation the up-grade carbohydrate-flux proceeds; the first stage of arrest we may attribute to the properties of sugar molecules themselves, while the final products of condensation are determined by the minute chemical configuration of the protoplasmic agents in contact with which this condensation proceeds.

REFERENCES

J. U. Nef. Various papers. *Annalen der Chemie*, Bdn. **357**, **376** and **403**.

H. A. Spoehr. The Carbohydrate Economy of the Cacti, 1919. *Carnegie Institution Publications*, No. 287.

D. T. MacDougal, H. M. Richards and H. A. Spoehr. Basis of Succulence in Plants. *Botanical Gazette*, **67**, 405. 1919.

A. Meyer. Über die Assimilationsproducte der Laubblätter angiospermer Pflanzen. *Bot. Zeit.* p. 415. 1885.

H. Winkler. U. über die Stärkebildung in den verschiedenartigen Chromatophoren. *Jahr. f. wiss. Bot.* **32**, 525. 1898.

H. Lundegardh. Einige Bedingungen der Bildung und Auflösung der Stärke. *Jahr. f. wiss. Bot.* **53**, 421. 1914.

E. T. Reichert. The Differentiation and Specificity of Starches in relation to genera, species, etc. 2 pts. 1913 *Carnegie Institution Publications*, No. 173.

—— A biochemic basis for the study of problems of Taxonomy, Heredity, Evolution, etc. with special reference to the Starches and Tissues of parent-stocks and hybrid stocks, and the Starches and Hæmoglobins of varieties, species and genera. 2 pts. 1919. *Carnegie Institution Publications*, No. 270.

HETEROTHALLISM AND SIMILAR PHENOMENA

By E. M. CUTTING

In 1906 *The New Phytologist* published a critical *résumé* of work (5) by A. F. Blakeslee on the presence of two kinds of mycelia in certain forms of Mucorine fungi. Since that date there have been accumulating a certain number of new facts bearing on the problem presented by the communication mentioned above. It is the purpose of this note to review shortly these disconnected observations and to attempt to indicate certain points of contact between them.

Of these, one of the most interesting is contained in a preliminary note by Burgeff (12), followed by a fuller illustrated account, in *Flora*, 1914 (13). This author worked mostly on *Phycomyces nitens*, a species that had previously been investigated by Blakeslee, who found that it possessed + and − forms, or in other words, was heterothallic. By means of a very delicate and difficult technique "grafting" was accomplished between a + and a − form of mycelium. The mycelial outgrowths resulting from this operation formed sporangia, which contained three kinds of spores, those which gave rise to + mycelia, those that formed −, and those that formed neutral hyphæ. These results were regarded as in keeping with the view, which is the one held by Burgeff himself, that the "plusness" or "minusness" resides in the nuclei themselves. The spores of *Phycomyces*, it will be remembered, are multinucleate and it is held that the neutral strain is formed when − and + nuclei are present in about equal numbers.

Blakeslee (6) has stated that in the heterothallic Mucors, so far as his investigations carried him, the zygospores germinated to form a sporangium which contains either + or − spores, so that a segregation occurs before the formation of sporangial spores. There was no evidence to show the method of this segregation. In *Phycomyces nitens*, however, the germ-mycelium was neutral and bore sporangia containing spores which gave rise to plus, minus and neutral mycelia; and the neutral mycelium had the power of forming abortive or imperfect zygospores with either − or + mycelia.

The experimental results of Burgeff fill in a gap in the observations given above. We have here, seemingly, a vegetative segregation caused by a differential nuclear distribution.

Blakeslee himself recorded in 1915 the formation of so-called imperfect hybrids, *i.e.* the partial union of reproductive bodies, when he grew diœcious species of *Zygorhynchus* between a + and a − *Mucor* (9, 10). The plus form showed imperfect fusions with the larger gamete of the *Zygorhynchus*, and the minus form with the smaller. On these grounds the plus race is regarded as the male-bearing thallus and the minus race as the female. The same opinion had already been expressed by Blakeslee from other considerations. It is a debated point whether these gametes of *Zygorhynchus* can be regarded as male and female in the usual sense, for it has been claimed that the contents of the larger cell are emptied into the smaller cell. Gruber (25) regards the larger as male and compares the process with that taking place in the Oomycetes. These results obtained by Gruber have been criticised by Moreau (34) who is of the opinion that the process in *Zygorhynchus* falls into line with the rest of the Mucorines, and that Gruber has erred through misinterpreting the position of the suspensor.

A point of further interest arises when it is found that G. F. Atkinson (1) holds that the larger cell in *Zygorhynchus*, supposed by him to be female, is provided with a trichogyne by means of which connection is made with the male organ, the smaller gamete. Atkinson also holds that *Zygorhynchus* is a lowly form of Ascomycete and a connecting bridge between this group and the Zygomycetes. It is not our purpose here to discuss the origin of any fungal group, but if *Zygorhynchus* be regarded as an Ascomycete the partial fusions with heterothallic Mucorines are even more difficult to explain.

A similar cross-septum has been reported in *Zygorhynchus* by Gruber (25), who also comments on its temporary nature but attempts no morphological interpretation. Further cytological observations should clear up these difficult points.

Burger (14) has recently been working on strains of *Cunninghamella*. He was unable either to get his results to fit those of Blakeslee or to suggest an alternative theory. I have specially mentioned this work for it is probably through an examination of such aberrant cases that further light will be thrown on the whole problem. Careful cultural experiments with species having uninucleate spores (and occasional multinucleate ones), and a comparison with multinucleated spore species, especially with regard to their heterothallism and heterogamy, would probably be helpful also.

No attempt will be made here to deal with the question of the methods of reproduction amongst the Myxomycetes. The Oomycetes,

however, which we will now consider, have been regarded by Clinton as showing indications of the presence, amongst them, of physiological strains (16, 17).

This observer found in cultures of different species of *Phytophthora* an abundant formation of oospores, interpreted by him as hybrids, at the place of intersection of the hyphæ. Murphy, working on *Phytophthora erythroseptica*, found a similar formation of oospores where neighbouring growths of hyphæ met, and, at first, was inclined to think that he was dealing with a heterothallic form (35). Single hyphal cultures, however, were capable of fruiting alone when any check was made to the further growth of the fungus, as by cutting out a piece of the medium in the track of growth of the hyphæ, oospore-formation immediately began. Murphy holds, therefore, that the phenomena observed by him was due to a nutritional check to the vegetative growth, initiating the sexual reproductive phase, and he thinks that Clinton's results, mentioned above, can be explained in a similar way.

Such interruptions do not necessarily induce an increased formation of reproductive bodies amongst the fungi.

Fitzpatrick has been investigating the origin of the binucleate condition in *Eocronartium muscicola*, a member of the Auriculariales; the germination of the uninucleate spores did not offer any solution, nor did an examination of its mycelium in one of the host plants give any further insight, as all the cells were binucleate (22, 23). There were no clamp-connections, however, so that it was not possible for migrations to take place there similar to those observed by Kniep in *Corticium varians* Kniep and *C. serum* Pers. The cross-walls of *Eocronartium* are provided with metachromatic granules and in the large number of fungi, in which such granules are found so associated, it is also usual to find a pore in the cross-wall. It is possible that migrations in *Eocronartium* and similar Basidiomycetes may take place through such pores, as such migrations have been reported amongst the Ascomycetes (18, 26, 43). The only function that was widely accepted for the clamp-connections before this work of Kniep's was that they facilitated the nutritive relations of the component cells of the hyphæ.

Kniep, it should be mentioned, has also found that a hypha after forming a basidium may go on growing and forming other basidia, in a manner which strikingly suggests a comparison with the account of the ascal-formation in *Pyronema*, as given by Claussen; and, in fact, Kniep does hold that the ascus and basidium are homologous

structures. The whole series of arguments may be profitably studied in his papers (29, 30, 31).

The opinion of Maire and of Miss Nichols (36), it may be remembered, is that, in the forms investigated by them, the binucleate conditions arose by simple division from the uninucleate condition. This may well be in some forms. Kniep, some few years ago, showed that in *Armillaria mellea*, basidia can arise on a uninucleate mycelium, so that here the conjugate stage is entirely left out (28). Miss Bensaude (3, 4), in a preliminary statement has briefly recorded her observations on an unnamed species of *Coprinus*, and her full thesis has since appeared: in this she describes the development of *Armillaria mucida, Tricholoma nudum*, and especially of *Coprinus fimetarius*. The hyphæ of the mycelium formed from a single spore exhibited anastomoses, but no clamp-connections, and never gave rise to the binucleate condition nor did they form fruit bodies. With mixed sowings, however, migrations take place after cell-fusions, the fusions being between mycelium and oidium or another mycelium; and in this manner the binucleate condition is brought about. Miss Bensaude is therefore of the opinion that the species of *Coprinus* investigated by her is heterothallic like some of the Mucors. Brefeld was able to grow fruit bodies, of another species of *Coprinus*, from one spore, so that Miss Bensaude does not expect that the method discovered by her will be found to be general among the Higher Basidiomycetes. The way in which the nuclear association is brought about reminds one of the similar process in *Humaria rutilans* (24)—except that here nuclear fusions immediately follow the binucleate condition—and more especially of the state of affairs in the Uredineæ (37) and in the Hemibasidii (2), in some of which the conjugate condition continues for a considerable period. No phenomena suggesting the occurrence of heterothallism have been met with in the Uredineæ, Bunts or Smuts.

In one genus of the Ascomycetes a phenomenon that seems allied to heterothallism has been found by Edgerton (20, 21). Here what had been formerly regarded as two different species of *Glomerella* are found to produce a larger number of fruits than are formed by either mycelium alone and under conditions that do not seem to point to hybridization.

This fungus forms but few ascocarps in the minus mycelium and the asci are small; a considerable number of asci are formed on the plus mycelium; at the junction of the two kinds of mycelium the perithecia form abundantly and contain large, well-developed asci,

the spores of which give rise some to + and some to − mycelia. This causes Edgerton to regard the formation of perithecia at the junction of + and − mycelia as being consequent on a sexual act. We are, however, quite ignorant of the method of origin and development of the ascocarp in this form and it is to be hoped that some information on this subject will soon be forthcoming. Shear and Miss Wood (39) have investigated this *Glomerella* and are of the opinion that hybrids are formed. Edgerton, as already mentioned, finds himself unable to accept this view. A side issue, but an important one, is to be found in the fact that this fungus is a parasite and the presence of both strains in a district would probably cause a larger spore-formation and so indirectly lead to greater destruction than if one form only were present. It will be seen that, whatever the cytological examination of these forms may result in, the case of *Glomerella* differs from all those so far described in that both its strains can form ascal-producing fruits; the result of the presence of both being that a greater number of ascocarps than usual are produced.

A case which, in a way, seems to resemble this, has lately been shortly described by Taubenhaus (42). In *Sclerotium rolfsii* there were indications of the formation of abundant sclerotia when certain kinds of mycelia met, these sclerotia differed in no ascertainable way from the sclerotia formed on any other mycelium and we might regard the phenomena here exhibited as being due to an interruption of vegetative growth, as in the case of oospores in *Phytophthora erythro-septica*, described by Murphy (35), were it not that Taubenhaus does not get the phenomena to take place at the point of contact of any kind of mycelial growth. This worker was unfortunate enough to have his cultures destroyed, by mistake, when he was away at war-work, and was unable to follow the matter any further on his return. It will be difficult to get an explanation of this behaviour, *i.e.* the abundant formation of, presumably, vegetative resting bodies, which will also include the other cases mentioned above.

In various other Ascomycetes, *e.g.* in *Diaporthe Batatatis* (27) and in *Gibberella Saubinetii* (Dickson and Johann (19)) various strains have been recorded, and in the Basidiomycetes considerable difficulties have been encountered in bringing them into fruiting stages. In these cases, where external conditions are not the factors concerned, as well as in the Fungi imperfecti, the observations of Miss Bensaude and of Edgerton point to a new manner of tackling the problem of obtaining the higher fructifications.

University College, London, *October* 1920.

REFERENCES

(1) Atkinson, G. F. The Morphology of *Zygorhynchus* and its relation to the Ascomycetes. *Science*, N. S. **35**, p. 151. 1912.

(2) Bartlett, A. W. The Hemibasidii. *New Phytologist*, **12**, p. 358. 1913.

(3) Bensaude, Matilde. Sur la sexualité chez des Champignons Basidiomycètes. *Comptes Rendus*, **165**, pp. 286–289. 1917.

(4) —— Recherches sur le cycle évolutif et la sexualité chez les Basidiomycètes. *Dissertation*, pp. 156, Pls. 13, figs. 30. Nemours, 1918.

(5) Blackman, V. H. The "sexuality" of the Mucorineæ. *New Phytologist*, **5**, p. 215. 1906.

(6) Blakeslee, A. F. Zygospore Germinations in the Mucorineæ. *Annales Mycologici*, **4**, No. 1. 1906.

(7) —— Papers on Mucors. *Bot. Gaz.* **47**, pp. 418–423. 1909.

(8) —— Conjugation in the Heterogamous Genus *Zygorhynchus*. *Mycologisches Centralblatt*, **2**, pp. 241–244. 1913.

(9) —— A possible means of identifying the sex of + and – races in the Mucors. *Science*, N.S. **37**, pp. 880–881. 1913.

(10) —— Sexual Reactions between Hermaphroditic and Diœcious Mucors. *Woods Hole Biol. Bull.* **29**, pp. 87–102. 1915.

(11) Brooks, F. T. Observations on pure cultures of some Ascomycetes and Basidiomycetes. *Trans. Brit. Mycol. Soc.* 1913.

(12) Burgeff, H. Über Sexualität, Variabilität und Vererbung bei *Phycomyces nitens*. *Ber. d. deut. bot. Gesell.* **30**, pp. 679–685. 1912.

(13) —— Untersuchungen über Variabilität, Sexualität und Erblichkeit bei *Phycomyces nitens* Kuntze. *Flora*, Bd. **108**, pp. 353, 448. 1914.

(14) Burger, F. O. Sexuality in *Cunninghamella*. *Bot. Gaz.* **68**, p. 134. 1919.

(15) Claussen, P. Zur Entwicklungsgeschichte der Ascomyceten, *Pyronema confluens*. *Zeitschr. für Bot.* **4**. 1912.

(16) Clinton, G. P. Artificial cultures of *Phytophthora* with special reference to oospores. Pt. 2. *Biennial Report*, 1907–8, *Connecticut Agric. Exp. Station*, pp. 891–907, Pl. 6. 1909.

(17) —— Oospores of Potato Blight—*Phytophthora infestans*. *Biennial Report*, 1909–1910, *of the Connecticut Agric. Exp. Station*, pp. 753–774, Pl. 3. 1911.

(18) Cutting, E. M. On the Sexuality and Development of the Ascocarp in *Ascophanus carneus*. *Ann. Bot.* **23**, p. 399. 1909.

(19) Dickson, J. G. and Johann, H. Production of Conidia in *Gibberella Saubinetii*. *Journal of Agric. Research*, **19**, p. 235. 1920.

(20) Edgerton, C. W. Plus and Minus Strains in the Genus *Glomerella*. *Am. Jour. of Bot.* **1**, pp. 244–254. 1914.

(21) —— Plus and Minus Strains in an Ascomycete. *Science*, N. S. **151**. 1912.

(22) Fitzpatrick, H. M. The Life-history and Parasitism of *Eocronartium muscicola*. *Phytopathology*, **8**, pp. 197–208, Pt. 1. 1918.

(23) —— The Cytology of *Eocronartium muscicola*. *American Jour. of Bot.* **5**, p. 398. 1918.

(24) Frazer, H. C. I. Contributions to the Cytology of *Humaria rutilans*. *Ann. Bot.* **22**, p. 35. 1908.

(25) Gruber, E. Einige Beobachtungen über den Befruchtungsvorgang bei *Zygorhynchus Moelleri* Vuill. *Ber. d. deut. bot. Gesell.* **30**, pp. 126–133. 1912.

(26) Harper, R. A. Über das Verhalten der Kerne bei der Fruchtentwicklung einiger Ascomyceten. *Jahrb. für wiss. Bot.* **29**, p. 656. 1896.

(27) Harper, R. A. and Field, E. C. "A dry rot of Sweet Potatoes caused by *Diaporthe Batatatis*." *U.S. Dept. Agric. Bur. of Plant Industry, Bull.* 281.

(28) Kniep, H. Über das Auftreten von Basidien im einkernigen Mycel von *Armillaria mellea* Fl. Dan. *Zeitsch. für Bot.* **3**, pp. 529–553. 1911.

(29) Kniep, H. Beiträge zur Kenntnis der Hymenomyceten. I, II. *Zeitsch. für Bot.* **5**, pp. 593–637. 1913.
(30) —— Beiträge zur Kenntnis der Hymenomyceten. *Zeitsch. für Bot.* **7**, pp. 369–398. 1915.
(31) —— Beiträge zur Kenntnis der Hymenomyceten. *Zeitsch. für Bot.* **8**, p. 352. 1916.
(32) Levine, M. Studies in the Cytology of the Hymenomycetes. *Bull. Torr. Bot. Club*, **11**, pp. 137–181. 1913.
(33) —— The Life-history and Sexuality of the Hymenomycetes. (Review.) *Bot. Gaz.* **18**, p. 67. 1919.
(34) Moreau, F. Sur la Reproduction sexuelle de *Zygorhynchus Moelleri* Vuill. *Compt. Rend. Soc. de Biol.* **78**, pp. 14–15. 1912.
(35) Murphy, P. A. The Morphology and Cytology of the sexual organs of *Phytophthora erythro-septica* Pethyb. *Ann. Bot.* **32**. 1918.
(36) Nichols, S. P. The nature and origin of the binucleated cells in some Basidiomycetes. *Trans. Wisconsin Acad. of Sciences*, **15**, p. 30. 1904.
(37) Ramsbottom, J. Recent published Results on the Cytology of Fungus Reproduction. *Trans. Brit. Mycol. Soc.* 1911, 1912, 1913.
(38) Shantz, H. L. and Piemeisel, R. L. Fungus Fairy rings in Eastern Colorado and their effect on vegetation. *Jour. Agric. Research*, **11**. 1917.
(39) Shear, C. L. and Wood, A. K. "Studies of Fungus Parasites belonging to the genus *Glomerella*." *U.S. Dept. Agric. Bur. of Plant Industry, Bull.* 252. 1913.
(40) Smith, A. Lorrain. Sexuality in the Basidiomycetes. (A review of Miss Bensaude's (3) paper.) *Journ. Royal Micros. Soc.* p. 617. 1917.
(41) —— Sexuality in the Basidiomycetes. (A review of Miss Bensaude's Thesis.) *Journ. Royal Micros. Soc.* 1920.
(42) Taubenhaus, J. J. Recent Studies on *Sclerotium rolfsii* Sacc. *Jour. Agric. Research*, **18**. 1919.
(43) Welsford, E. J. Fertilization in *Ascobolus furfuraceus*. *New Phytologist*, **6**. 1907.
(44) Wollenweber, H. W. Identification of species of *Fusarium* occurring on the Sweet Potato. *Jour. Agric. Research*, **2**. 1914.

POSTSCRIPT

Since the above was written an important summary of non-cytological work on the sex of the Mucorineæ by Namyslowski has appeared in the *Revue Générale de Botanique* (May 1920). Amongst other interesting facts, our attention is drawn to the opinion, which seems to be growing prevalent, that a series of transitions exist between homothallic and heterothallic forms, and that external conditions greatly modify the character of the method of reproduction. Burger's results on *Cunninghamella* and the behaviour, reported by Edgerton, of the ascomycete *Glomerella*, are in keeping with this view, but not with that originally put forward by Blakeslee. It will be evident, moreover, from a general knowledge of plant physiology that the phenomena of "Zygotactism" and of "Haptomorphism" may be expected to vary much with external conditions, and the latter may indeed prove to be replaceable by some other stimulus.

SUBERIN AND CUTIN

By J. H. PRIESTLEY

Introduction

During an investigation of the physiological *rôle* of the endodermis it became necessary to describe the composition of the radial and transverse walls of this tissue, which from an early stage in their differentiation appear relatively impermeable to water. The impermeability to water of a plant membrane seems usually to have been ascribed to the presence within it of suberin or cutin, but in using these terms the writer was very conscious of the lack of precision with which he employed them. Reference to current English text-books revealed a similar vagueness even in the most recent monographs on plant biochemistry. However, a search through the literature showed, that during the last thirty years a great deal of light had been thrown upon the subject by the research of different continental investigators. The work seems so important and so neglected in this country that it is proposed to give a brief account of it in this paper.

Although this is a review of earlier work upon the subject, no lengthy bibliographical record is attempted, but reference to the papers cited will enable any reader to obtain the nucleus of an excellent bibliography. On the biochemical side Czapek's book (4), p. 695, contains a very valuable chronological summary. Here it is only possible to emphasise the most salient points in the development of our knowledge of the subject.

Most of our knowledge refers to suberin which is available for study in convenient form in the shape of bottle cork, the but little altered periderm of *Quercus suber*. Cutin receives elucidation usually indirectly as result of the work done upon suberin. So far, those substances are rather distinguished by their position in the plant, than by their properties, suberin being formed in the periderm, cutin in the outermost layer of many epidermal walls which are thus provided with a cuticle.

It will be seen from the account which follows that suberin and cutin, although still far from completely known, are names for aggregates of substance occurring in or on plant membranes and differing in their composition as well as in their distribution in the plant. The component substances of these aggregates have to some extent been

isolated and described and a suggestion can be made as to the form in which they are present within the wall. Furthermore, the ground seems clear for future work which may be expected to elucidate the nature and origin of the substances in the cell from which suberin and cutin are first formed, and also the conditions under which proceeds the transformation of these substances into suberin and cutin.

The following account is written with the more confidence because practically all observations which the present writer regards as fundamental have been repeated in his laboratory by different students. In this connection he has particularly to thank Miss M. Hind, B.Sc., Miss Edith North, B.Sc., Miss R. Rea, B.Sc., and Miss B. Lee.

Towards a Definition of Suberin—A Comparison with Lignin

The term suberin is due to Chevreul (2) and was given by him to a substance insoluble in water and alcohol and constituting seventy per cent. of the substance of bottle cork. This substance he regarded as responsible for the special properties of cork, impermeability to water, general insolubility and great resistance to acids, etc.

"Suberin" starts in the literature then as a substance generally responsible for the peculiar properties of cork, and it appears to have gained little in clearness in English botanical literature until the present time. The reason for this is easily seen. Most botanical investigations have followed the micro-chemical method in investigating cork. Naturally it has not been possible to get much further than that the substance which *appears* to give cork tissue or periderm its peculiar properties, is concentrated in a special lamella constantly present within the cell wall of the cork cell. To this substance or mixture of substances the name of suberin has been given by common consent.

The first full and clear description of the substance or substances in the lamella we owe to von Höhnel (9) whose work remains a landmark in the study of the subject, and it will be useful to cite briefly the characteristics of suberin as recognised in von Höhnel's monograph.

One difficulty has always been to distinguish suberin from lignin, as both lignified and suberised tissues are left behind by treatment with strong acids or cellulose solvents. Von Höhnel points out that lignin possesses many more characteristic colour reactions, a statement which is even more true to-day when beside those with phenol acid salts, many more general colour reactions for lignin are known. (See Czapek (4), p. 689.)

Von Höhnel attached most importance to the reaction of suberin with oxidising agents such as nitric acid or Schulze's macerating solution (potassium chlorate in nitric acid), a reaction which he describes as the cerin or cerinic acid reaction because the suberin is completely oxidised to a waxy substance which he regards as an oxidation product of suberin and terms cerinic acid; lignin gives no such oxidation product.

For micro-chemical purposes the sections are placed in Schulze's macerating solution and warmed gently under the coverglass, the lignified walls are gradually destroyed, the walls becoming more and more transparent and behaving like pure cellulose. Suberised (or cutinised) walls are much more resistant. They remain opaque and dark in the cold reagent and sharply contrasted therefore with all other walls; on warming an ebullition of gas is seen from the cork walls, but they swell very little until at a stage in the process of warming they collapse, the outlines becoming very wavy and swollen, the contents of the membrane largely melting up into oily masses which finally become spherical and globular and solidify on cooling. These globules are said to consist of cerinic acid, a substance first obtained by a similar process by Doepping (5). Doepping gave it the name, under the impression it had arisen by the oxidation of cerin, a substance found to a small extent in cork. Von Höhnel retains the name whilst giving very sound ideas for regarding it as an oxidation product of suberin.

Another reaction of great importance in the identification of suberin, as was also emphasised by von Höhnel, is its behaviour with caustic alkali. Both lignin and suberin dissolve in concentrated caustic potash on warming, but von Höhnel points out that the suberin containing wall is usually thrown into more marked disorganisation by the removal of the suberin, which gradually disappears from the wall on heating, usually going into solution with a strong yellow colour. The lignin dissolves out in a very different way, leaving the wall little altered by its departure; in the solution of lignin a marked yellow coloration is often observed so that too much importance cannot be attached to this colour change.

Anticipating later work this distinction may be emphasised. In the lignified membrane lignin and cellulose seem to be present in an intimate physical mixture[1], and after solution of the lignin the outline of the wall remains practically unchanged. But in the cork wall

[1] The reader is referred for recent evidence on this point to the very interesting paper by Robinson (13).

the suberin seems to form an intermediate median lamella *unmixed with cellulose*, and its solution is accompanied by a distortion of the inner cellulose wall which is often left free in the interior of the cell.

In stating this we are travelling beyond von Höhnel who considered that when the suberin had been removed from the lamella a basis was left behind consisting of cellulose. His main argument for this belief is that after and during the treatment with potash the suberin containing lamella gave a violet or reddish-violet reaction with iodine or sulphuric acid or with chlor-zinc-iodine, a reaction that he considered due to the cellulose present when it is no longer masked with suberin.

We owe to von Höhnel the conception that the normal cork wall consists of three layers—the outermost or the middle lamella, a median one or the suberin lamella, and an inner one of cellulose. All subsequent investigators have confirmed this conclusion, but one of the most careful of them, van Wisselingh (15), has modified von Höhnel's description in one important particular. Von Höhnel described the median lamella as suberin on a basis of cellulose, van Wisselingh describes it as suberin without admixture of cellulose. Before describing van Wisselingh's work, however, it will be desirable to describe some macro-chemical observations of Eugène Gilson (8). Van Wisselingh's observations, made with great care and precision, are entirely micro-chemical in nature. They are published in a long series of papers which were appearing during the time that Gilson's work was published.

Gilson's work, dealing with appreciable quantities of material by the normal manipulations of organic chemistry, threw great light on the nature of suberin and incidentally enabled van Wisselingh to assess the critical value of his own micro-chemical observations with much more confidence.

The Macro-Chemical Investigation of Suberin

Gilson's work is based upon the solution of suberin on warming with potash. Recognising that the process was probably accompanied by the formation of soluble potassium salts of organic acids as in the saponification of an ester or true fat with alkali, he proceeded, by the customary methods of organic chemistry, to attempt the isolation of any organic acids and alcohols that might be present in solution.

As suberin seemed to dissolve more completely in an alcoholic solution of potash, he carried out his original saponification of powdered bottle cork with three per cent. alcoholic potash.

His original paper must be consulted for details of his methods, but the results may be summarised as follows:

He established the presence of several organic acids, which he termed as a class the *suberogenic acids*. Some of these acids, notably *phellonic* acid and *phloionic* acid, he obtained pure and crystalline. He found traces only of one higher alcohol, glycerine, and gave reason for thinking that the suberogenic acids were present in suberin in other forms than that of glycerides.

Gilson gives full details of his manipulatory methods, which have been followed throughout in a repetition of the work in the laboratory by several workers. His statements have all been confirmed even as to approximate yield obtained, save that so far we have failed to isolate sufficient quantities of glycerine to obtain the crystalline glycerine tribenzoate with benzoyl chloride and thus place beyond doubt the production of glycerine as a result of saponification.

In any case, Gilson concluded from the small quantities of glycerine obtained on saponification, and from the insolubility of the original suberin in normal fatty solvents, that suberin could not be regarded as a typical fat.

Kügler (11) had previously shown that some 12 per cent. of solid matter could be extracted from cork by boiling chloroform, of which some 2·9 per cent. was the crystalline substance cerin previously referred to (p. 19). The rest of the substance extracted proved to be amorphous and Kügler considered it to be suberin. Explaining his inability to extract the rest of the suberin by assuming that it was protected from the action of the fatty solvent by the molecules of cellulose which enveloped it, and assuming solubility of suberin in fatty solvents, Kügler decided that it was to be regarded as a true fat.

Although suberin is known to stain with fatty stains—notably Sudan III (see Kroemer (10) for an elaboration of this staining method) and Scarlet Red (Scharlach R)—Gilson's conclusion above seems soundly based and suberin cannot be regarded as a true fat[1]. There remain two outstanding questions, in what form are the suberogenic acids present in suberin and do they unite in the formation of a single definite substance suberin or is suberin an aggregate formed from varying quantities of these suberogenic acids?

As already stated Gilson obtained two of these acids crystalline

[1] Schmidt (14) has confirmed the presence of a small proportion of glycerides in suberin and suggests that the suberogenic acids originally reach the lamella in this form, subsequently decomposing and releasing the suberogenic acids.

and pure, viz. phellonic acid M.P. 95–96° C., percentage composition suggesting the formula $C_{22}H_{43}O_3$, and phloionic acid, crystallising in fine white needles, M.P. 120–121° C., percentage composition varying with prolonged drying from $C_{11}H_{21}O_4$ to $C_{22}H_{40}O_7$.

Another amorphous substance, semi-liquid, which Gilson terms suberinic acid, was obtained in relatively large quantities and, if it can be regarded as pure, its composition would agree with the formula $C_{17}H_{30}O_3$.

Of these suberogenic acids, phellonic was most completely studied, being obtained relatively easily in considerable quantities in the pure state, but all three acids possess one very important property. Both the acid and some of the salts, on heating for some time in sealed tubes, tend to go over into other forms, possibly anhydride or condensation products, which differ materially from the original suberogenic acid. The latter is soluble in the usual fatty solvents, at any rate on warming, the anhydrides are quite insoluble; the acid or some of its salts may be soluble or at least have a tendency to swell in water, whilst the new product is quite unaffected by the presence of water.

The significance of these facts for the formation of suberin is obvious. An experiment which has been carried out successfully in the laboratory gives an excellent demonstration of the possible significance of the suberogenic acids in the formation of impermeable membrances.

An ordinary Soxhlet thimble, as used in fat extractions, consists of a fat free cellulose preparation, readily permeable to water. One of these thimbles was taken and impregnated with a concentrated solution of potassium phellonate in hot chloroform. The thimble was then dried until all the chloroform had evaporated and then sealed up in a wide glass tube after partial exhaustion by a Geryk air-pump.

This sealed tube was then heated to about 180° C. on successive days for a total of about twenty-four hours in all. The phellonate in the thimble partly volatilised on to the walls of the tube but enough was left to impregnate the thimble thoroughly with the resulting anhydride or condensation product.

After heating, the potassium phellonate could no longer be removed from the thimble by the action of boiling fatty solvents and was obviously altered in its nature. This new substance rendered the Soxhlet thimble completely impermeable to water, the outer surface remaining quite dry to the touch when the thimble was filled to the brim with water and left for several hours.

It thus appears that it is possible to prepare artificially condensation products of these suberogenic acids and their salts which have the reactions that have been cited as characteristic of suberin; and that these acids can be obtained from suberin by saponification. The conclusion is then rendered probable that suberin consists largely of anhydrides of these acids, possibly together with a small proportion of the acids combined with glycerine as glycerides or true fats.

Von Höhnel, and Fremy (6) before him, spoke of suberin and cutin as definite individual substances, but it is obvious in the light of Gilson's work that they are more probably aggregates or mixtures differing in their composition with variations in the original proportions of the suberogenic acids from which they are formed.

This is indeed the case, for Gilson himself showed that the cork of *Ulmus "suberosa"* differed in its constituent suberogenic acids from that of *Quercus suber*, phellonic acid, present in considerable quantities in the cork of the latter being quite absent from that of the former.

Possibly these suberogenic acids may have a practical future before them in water-proofing cellulose fabrics (see Cross and Bevan (3), *loc. cit.* p. 235). Certainly they exist in nature in sufficient quantities if they are required; the Eriophorum peat deposits of Yorkshire consist largely of the preserved cuticle, endodermal and corky tissues of Eriophorum and some preliminary experiments by Miss Hind show that large quantities of these suberogenic acids can be readily obtained from this peat by saponification.

Micro-Chemical Investigations—No Cellulose Basis to Suberin or Cutin Lamella

For the clear recognition of the difference between cutin and suberin, and between the suberin of different species, we must turn to van Wisselingh's papers (15–18).

Van Wisselingh's methods need studying in the original papers, and show how much insight into the ultimate structure of the membrane can be obtained in spite of the limitations of micro-chemical technique. The basis of this method was a study of the progressive decomposition or melting of the suberin lamella under four different methods of treatment: (1) heating in pure glycerine over a range of temperature, the highest well above 300° C., (2) heating in glycerine after previous treatment in concentrated potash (50 per cent.), (3) heating over the same range of temperature in glycerine containing 10 per cent. potash, (4) warming in 10 per cent. alcoholic potash.

Van Wisselingh tried all these methods on the tissues of certain selected plants and compared carefully the widely differing results he obtained. It would take too long to show how, by careful comparison of one series of results with another, he gradually arrives at conclusions as to the nature of the suberin or cutin in the particular plants under investigation, conclusions which seem to the present writer very critically established.

We must confine ourselves to two general conclusions of van Wisselingh's, first that the suberin lamella has no basis of cellulose, secondly that the suberin and cutin are not definite substances but varying aggregates.

Van Wisselingh, repeating von Höhnel's observation that the suberin lamella during treatment with potash began to give staining reaction with iodine and sulphuric acid or with chlor-zinc-iodine, had already published (16) his reasons for doubting whether this reaction could be due to cellulose. Gilson later published his paper, describing the isolation of phellonic acid (see p. 21) and showed that both phellonic acid and its salt gave red to red-violet coloration with the iodine reagents used and suggested that von Höhnel had been misled by the production of phellonic acid during the saponification of the suberin by potash. Van Wisselingh then returned to the subject (17); he showed that the coloration with iodine during treatment of the lamella with potash is a transient phenomenon, whilst cellulose would remain during this treatment; he further showed that after complete removal of the suberin, either by heating to 300° C. in glycerine or by saponification in 10 per cent. alcoholic potash or 10 per cent. glycerine potash, the suberin lamella gives no trace whatever of cellulose, and he gave further reasons for thinking that the reaction occasionally obtained is due either to phellonic acid or its salts or possibly in some cases to yet another suberin constituent.

Similarly, van Wisselingh gave reasons for considering that in the case of the cuticle, where we have present a layer of cutin and beneath that the so-called "cutinized lamella," where cutin-like substances are deposited in a cellulose layer, the upper layer of cutin is entirely devoid of a cellulose basis.

Considerable emphasis is laid upon these conclusions, which seem to the writer to be well founded. They indicate a point of view which must be taken into account by plant pathologists when considering the entry of parasitic fungi through the uninjured plant surface or when discussing the possible effect of spray fluids on the plant they protect.

Most parasitic fungi contain cytases, or cellulose dissolving enzymes, which are excreted at the growing tips and could probably disintegrate a membrane with a cellulose basis, as for instance many wood-destroying fungi disintegrate lignified membranes without digesting the lignin. But unless a fungus hypha penetrates through stoma or lenticel, it finds itself met at the surface of the plant by an unbroken lamella containing no cellulose fabric at all and which is chemically so composed that it would seem unlikely that ordinary hydrolysing enzyme action would decompose it.

It is therefore interesting to note that Blackman and Welsford (1) in the case of the parasitic fungus Botrytis, describe it as appearing to penetrate the cuticle by forcing its pointed tip forward under hydrostatic pressure, so that it wins its way through by mechanical displacement of the actual waxy substance of the cuticle.

The absence of cellulose in the external layers of the plant is a conception that does not seem to find favour with English writers, but possibly too much weight has been attached to the criticism of Cross and Bevan (3) (*loc. cit.* p. 228). The views expressed in this English monograph, where cork is described as an "adipo-cellulose" or fatty substance allied to cellulose, are quoted in all English biochemical texts. Cross and Bevan briefly state van Wisselingh's point of view (although they quote him as "van Wissenburgh") and then brush it aside because, after removal of the suberin from cork by a special bisulphite process used on a macro-chemical scale, cellulose is indisputably present in the residue. But this is entirely beside the point. Reference to van Wisselingh's papers will show his frequent description of cellulose layers within cork cells, *internal* to the suberin lamella. The only point at issue is whether cellulose also occurs within the suberin lamella itself.

Van Wisselingh gives reasons, that seem very adequate, for concluding that it does not, and this being the case it will follow, unless the middle lamella has a cellulose basis, that the cork will provide an unbroken cellulose-free layer just as the cuticle does.

Suberin and Cutin not Chemical Entities but Aggregates of Substances

Van Wisselingh concludes that suberin is a mixture of substances because in his observations he sees these substances melting out of the lamella at different temperatures. In general he recognises two series of substances as present; the one series, melting at relatively

low temperatures and soluble to a large extent in boiling chloroform, he is inclined to regard as true fats; the other series, melting at higher temperatures or even decomposing before melting, or melting at lower temperatures after previous saponification, he would identify with the anhydride or condensation products of the suberogenic acids. But the mixture differs from plant to plant as might be expected. It has been possible to confirm one micro-chemical observation by macro-chemical methods. Van Wisselingh (17) describes the periderm of *Salix caprea* as remarkably aberrant under treatment by his method and notes that it never gives any indication of phellonic acid. Miss Rea has extracted the ground-up periderm of *Salix caprea* by Gilson's method and finds that no potassium phellonate at all can be identified in the alcoholic extract after saponification.

Cutin has not been so fully examined as suberin, but it is worthy of note that long prior to Gilson's work, Fremy and Urbain (7) as the result of the saponification of cutin (or "cutose" as they termed it) had obtained two organic acids that they described as "stearocutique" and "oleocutique." They had failed to identify any alcohol with which these acids were combined prior to saponification, and had noticed the tendency of these acids under various conditions to undergo profound modification in their properties, such as losing their solubility in fatty solvents, and in the case of the solid acid "stearocutique" a rise of melting point.

These reactions certainly suggest "cutinogenic acids" transformed in the formation of cutin in the same way as suberogenic acids are modified in forming suberin.

Furthermore, cutin, examined by van Wisselingh's method, can be shown to contain no trace of phellonic acid though other "cutinogenic" acids are present; this observation also is supported by some preliminary macro-chemical observations made by Miss B. Lee. In one case van Wisselingh (17 and 18) examined at different times the cuticle and periderm of the same plant, *Ilex aquifolium*, and a comparison of the results will show that in the same plant the substances forming cutin and suberin respectively do not seem to be identical.

We thus reach the conclusion that suberin and cutin are names for aggregates of substances which present certain characters in common, suberin being present in the median lamellæ of the walls of periderm cells and cutin as a continuous layer on the outside of the cuticle and in dispersed patches throughout the cutinised lamellæ below when these are present.

These substances consist of aggregates of organic acids, the suberogenic (or cutinogenic) acids, which are present to a small extent as glycerides or true fats, to a greater extent as condensation products or anhydrides of the acids. The differences between the suberin and the cutin of different plants, or between these two substances within the same plant will be due, in part to differences in their constituent acids, and in part to differences in the external and internal conditions prevailing whilst these acids pass over into the form that they assume in the mature suberin or cutin lamella.

A consideration of the work described above indicates many avenues of research opening before the investigator. On the one hand, only extended observation in which macro-chemistry and micro-chemistry both take their share can put the detailed knowledge of suberin and cutin on a broad basis, and until that is done the view outlined above, however satisfactory as an explanation, cannot be regarded as having a sufficient experimental basis.

On the other hand questions are suggested as to the methods by which the original lamellæ of suberin and cutin were formed. The acids described here as suberogenic are too empirically known yet to permit an elucidation of their constitution, though presumably they will readily admit of chemical derivation from some of the carbohydrates found within the plant (though by no means necessarily from celluloses).

The origin of the suberogenic acids has to be traced, and then we have to ascertain under what conditions in the plant these substances can assume the impermeable form, insoluble in fatty solvents, in which they are present in the mature suberin or cutin lamella. These conditions will be different from the methods of heating in sealed tubes adopted by Gilson and are probably already indicated by some of the literature referring to the conditions under which cork walls and cuticle are formed. It is for example very fascinating, in the light of the views expressed above, to read such a summary as that provided by Küster (12) of the conditions under which wound cork is formed, and to see that some conditions favour the early and extensive deposit of suberin on the cell arising from the newly formed meristem, whilst other conditions appear to impede its formation.

SUMMARY

1. Suberin is the name given to a substance present in the median lamella of the wall of periderm cells, between the middle lamella outside and the cellulose layer within; to this substance the

special properties of periderm, impermeability to water and resistance to sulphuric acid, are supposed to be due.

2. Cutin is a substance present as a continuous external lamella on the outer wall of the epidermis in leaf and stem to which is assigned the same *rôle* in reference to the cuticle.

3. The properties of these suberin and cutin layers may be jointly defined as insolubility in and impermeability to water, considerable insolubility in fatty solvents, great resistance to concentrated sulphuric acid, ready oxidation by nitric or chromic acids and ready solubility in warm alkali; they are stained by fat stains such as Sudan III or scarlet red.

4. In the layers in which suberin or cutin are present in the plant wall no cellulose can be detected; the importance of this conclusion to students of plant pathology is emphasised.

5. On chemical grounds suberin may be regarded as an aggregate of variously modified forms (condensation products or anhydrides) of certain organic acids, the suberogenic acids. The chemical constitution of these acids requires further elucidation before the problem of the origin of the suberogenic acids can be satisfactorily attacked.

To a small extent the suberogenic acids may be present in suberin in combination with glycerine as substances of the nature of true fats.

6. These suberogenic acids, some of which have been obtained crystalline and in the pure state, are usually soluble in fatty solvents at any rate on warming, but the anhydrides or condensation products formed from them are completely insoluble in fatty solvents and only give rise to the original suberogenic acids on saponification with alkali.

7. One of these suberogenic acids, phellonic acid, gives colour reactions with iodine reagents which are responsible for the erroneous impression that cellulose is present in the suberin lamella.

8. There is not the same experimental evidence in the case of cutin, but there is every reason for thinking that this is a similar aggregate of modified forms of "cutinogenic" acids.

9. Differences between suberin and cutin of different plants, or between the suberin and cutin of the same plant may be traced (1) to different organic acids and different proportion of those acids entering into the composition of the aggregate, (2) to the different conditions under which these acids have been transformed into the modified form in which they are present in the mature aggregate.

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REFERENCES

(1) Blackman, V. H. and Welsford, E. J. Studies in the Physiology of Parasitism. II. Infection by *Botrytis cinerea*. *Annals of Botany*, **30**, p. 389. 1916.

(2) Chevreul. *Annales de Chimie*, **96**, p. 141. 1815.

(3) Cross and Bevan. *Cellulose*. London, 1916.

(4) Czapek, F. *Biochemie der Pflanzen*, **1**, 2nd ed. 1913.

(5) Doepping. *Liebig's Annalen*, **45**, p. 286. 1843.

(6) Fremy, E. *Annales des Sc. Nat. Bot.* **13**, p. 353. 1876.

(7) Fremy, E. and Urbain. *Annales des Sc. Nat. Bot.* **13**, p. 360. 1876.

(8) Gilson, Eugène. La Subérine et les Cellules du Liège. *La Cellule*, **6**, p. 63. 1890.

(9) Höhnel, Franz von. Über den Kork und verkorkte Gewebe überhaupt. *Sitzungsber. der Math.-Naturwissensch. Classe der Kais. Akademie der Wissensch.* Wien, **76**, pp. 507–660. 1877.

(10) Kroemer, Karl. Wurzelhaut, Hypodermis und Endodermis der Angiospermenwurzel. *Bibliotheca Botanica*, **59**, p. 1. 1903.

(11) Kügler. *Über das Suberin.* Dissertation, Strasburg. 1884.

(12) Küster, E. *Pathologische Pflanzenanatomie*. Jena, Gustav Fischer. 1916.

(13) Robinson, W. The Microscopical Features of Mechanical Strains in Timber and the bearing of these on the structure of the cell-wall in plants. *Phil. Trans. Roy. Soc.* **210** B, pp. 49–82. 1920.

(14) Schmidt. Zur Kenntnis der Korksubstanz. *Monatshefte für Chemie*, **31**, p. 347. 1910.

(15) Wisselingh, van C. La Gaîne du Cylindre Central dans la Racine des Phanérogames. *Arch. Néerlandaises des Sciences exactes et naturelles*, **20**, p. 95. 1886.

(16) —— Sur la Paroi des Cellules subéreuses. *Arch. Néerlandaises, etc.* **22**, p. 253. 1888.

(17) —— Sur la Lamelle subéreuse et la Subérine. *Arch. Néerlandaises, etc.* **26**, p. 305. 1892.

(18) —— Sur la Cuticularisation et la Cutine. *Arch. Néerlandaises, etc.* **28**, p. 373. 1895.

STUDIES IN PHÆNOLOGY, No. 2, 1920.

By FRANCIS DARWIN.

This paper is a continuation of my "Phænological Study" published in Nos. 9 and 10 of *The New Phytologist*, **18**, November and December, 1919.

All my earlier observations (1917, 1918 and 1919) were made at Brookthorpe near Gloucester. The present series is indeed based principally on observations in that locality, but it also includes observations made at Cambridge and in the heathy country near Gomshall in Surrey.

The record of temperatures, which is the principal condition affecting the date of flowering, is (as in my former paper) taken from the "Weekly Weather Reports of the Meteorological Office." For the Gloucestershire observations I have taken the temperatures at Clifton, the observational centre nearest to Brookthorpe. For the Surrey observations I have taken the Wisley temperatures. For those in Cambridgeshire the temperatures at Cambridge.

Table I

Temperature from "Weekly Weather Report of the Meteorological Office," 1920.

Week no.	Week ending	Mean temp. F.	Deviation from normal	Week no.	Week ending	Mean temp. F.	Deviation from normal
1	Jan. 10	38·7	+1·1	18	May 8	49·9	−0·6
2	17	45·1	+7·9	19	15	53·6	+1·4
3	24	43·9	+6·3	20	22	52·8	−1·0
4	31	42·0	+3·7	21	29	61·9	+6·8
5	Feb. 7	41·5	+2·6	22	June 5	57·4	+0·2
6	14	44·6	+5·8	23	12	56·4	−1·8
7	21	43·5	+4·5	24	19	60·0	+2·0
8	28	39·1	−0·2	25	26	61·1	+1·5
9	Mar. 6	44·3	+4·6	26	July 3	61·2	−0·2
10	13	39·8	−0·7	27	10	56·9	−5·0
11	20	43·9	+2·3	28	17	59·2	−3·0
12	27	48·9	+6·8	29	24	59·5	−3·1
13	Apr. 3	48·1	+3·7	30	31	57·3	−4·9
14	10	(No record)		31	Aug. 7	57·1	−5·4
15	17	49·2	+2·7	32	14	59·4	−1·6
16	24	48·8	+1·0	33	21	56·8	−3·8
17	May 1	47·9	−1·6	34	28	54·7	−5·4

I have also given the 1918 temperatures as being of interest in connexion with the comparison of the flowering dates of that year with those of 1920.

1918				1918			
Week no.	Week ending	Mean temp. F.	Deviation from normal	Week no.	Week ending	Mean temp. F.	Deviation from normal
1	Jan. 5	34·1	−5·6	27	July 6	63·8	+1·9
2	12	36·5	−2·5	28*	13	58·1	−1·9
3	19	39·6	−0·1	29*	20	60·3	−0·4
4	26	50·1	+9·8	30	27	60·2	−2·0
5	Feb. 2	44·6	+3·9	31	Aug. 3	64·1	+1·6
6	9	48·5	+8·1	32	10	62·7	+0·5
7	16	46·7	+6·2	33	17	62·9	+1·1
8	23	40·9	+0·7	34	24	64·0	+2·9
9	Mar. 2	40·9	0·0	35	31	58·3	−1·6
10	9	39·0	−2·3	36	Sep. 7	58·9	−0·2
11	16	45·1	+2·5	37	14	55·5	−2·7
12	23	47·0	+4·3	38	21	58·1	+1·4
13	30	46·3	+1·9	39	28	53·2	−1·7
14	Apr. 6	46·1	+0·2	40	Oct. 5	48·9	−4·0
15	13	46·8	+0·3	41	12	52·0	+0·8
16	20	40·1	−7·7	42	19	46·5	−3·4
17	27	49·6	+0·1	43	26	47·7	−0·2
18	May 4	49·9	−0·6	44	Nov. 2	52·0	+4·5
19	11	54·2	+2·0	45	9	45·5	−1·0
20	18	57·3	+3·5	46	16	43·3	−0·8
21	25	62·4	+7·3	47	23	38·7	−4·4
22	June 1	60·9	+3·7	48	30	46·6	+3·6
23	8	61·0	+2·8	49	Dec. 7	51·7	+9·7
24	15	56·5	−1·5	50	14	49·8	+8·0
25	22	55·3	−4·3	51	21	44·5	+3·7
26	29	57·0	−4·4	52	28	42·0	+1·7

The most obvious feature in the conditions ruling in 1920 is the relatively high temperature of the winter and spring. Thus from Jan. 4 to March 27, *i.e.* 12 observations, there are only two cases of temperatures below normal, viz. Feb. 28, − 0·2 F.[1] and March 13, − 0·7; the temperatures above normal varying from + 1·1 to + 7·9.

In the list (Table II) which follows, the first column gives the locality of the observation: thus the plants marked C were found in Cambridgeshire; those marked S were found near Gomshall in Surrey. The remainder (not marked with a letter) were found near Brookthorpe in Gloucestershire. Then follow (in separate columns)

[1] By − 0·2 F. is meant a fifth of a degree below the daily mean temperature. The weeks are described by their later date, thus Feb. 28 means the week Feb. 21–28.

the current numbers of the observations (from No. 1 to No. 272), the date of observation and the name of the plant. Finally, for the sake of comparison, the flowering dates for 1917, 1918 and 1919 are given so far as they are available. Alongside these dates are placed the letters E and L, indicating earlier or later occurrence than in 1920.

Table II

No.	1920	Name	1917	1918	1919
1	Jan. 3	Ranunculus repens	—	May 10 **L**	May 15
C 2	8	Primula vulgaris	—	—	—
C 3	10	Tussilago petasites	—	—	—
C 4	21	Galanthus nivalis	—	—	—
C 5	22	Capsella Bursa-pastoris	—	—	—
C 6	Feb. 7	Ulmus campestris ♂	—	—	—
C 7	Mar. 3	Ranunculus Ficaria	Apr. 1 **L**	Feb. 10 **E**	Mar. 13 **L**
C 8	4	Lamium album	May 10 **L**	Feb. 16 **E**	Apr. 15 **L**
C 9	9	Taraxacum Dens-leonis	Apr. 25 **L**	Jan. 22 **E**	Mar. 15 **L**
C 10	11	Tussilago Farfara	—	Mar. 13 **L**	Apr. 5 **L**
C 11	21	Caltha palustris	Apr. 22 **L**	—	Apr. 9 **L**
12	24	Mercurialis perennis	—	♂ Fe. 4 **E**	♂ Mr. 14 **E**
13	24	Cardamine pratensis	May 2 **L**	Mar. 17 **E**	Apr. 7 **L**
14	24	Chrysosplenium oppositifolium	—	17 **E**	4 **L**
15	25	Fragaria vesca (wild)	Apr. 21 **L**	16 **E**	6 **L**
16	25	Lamium Galeobdolon	May 11 **L**	May 12 **L**	May 10 **L**
17	25	Oxalis acetosella	—	Mar. 16 **E**	Apr. 22 **L**
18	25	Primula veris	—	24 **E**	9 **L**
19	25	Nepeta Glechoma	May 2 **L**	21 **E**	12 **L**
20	26	Viola canina	—	—	22 **L**
21	27	Anemone nemorosa	—	Mar. 26 **E**	10 **L**
22	27	Viola odorata	—	13 **E**	Jan. 1 **E**
23	28	Lychnis diurna	—	Apr. 28 **L**	May 9 **L**
24	29	Scilla nutans	May 11 **L**	15 **L**	Apr. 22 **L**
25	29	Chærophyllum sylvestre	18 **L**	16 **L**	May 6 **L**
26	30	Stellaria holostea	11 **L**	14 **L**	Apr. 22 **L**
27	31	Alliaria officinalis	14 **L**	8 **L**	May 6 **L**
28	Apr. 4	Vicia sepium	12 **L**	30 **L**	15 **L**
29	5	Heracleum Sphondylium	—	May 11 **L**	20 **L**
30	8	Arum maculatum	May 10 **L**	—	Apr. 28 **L**
31	9	Lychnis diurna (plenty; see No. 23)	—	Apr. 28 **L**	May 9 **L**
32	10	Vinca minor	—	—	—
33	10	Ranunculus auricomus var. depauperata	May 10 **L**	Apr. 12 **L**	May 10 **L**
34	10	Lamium maculatum	—	—	2 **L**
35	10	Veronica Chamædrys	May 12 **L**	Apr. 29 **L**	10 **L**
36	11	Paris quadrifolia	—	—	14 **L**
37	13	Pedicularis sylvatica	May 6 **L**	May 24 **L**	7 **L**
38	14	Plantago lanceolata ♀	12 **L**	Apr. 14 =	—
39	15	Acer Pseudo-platanus	6 **L**	May 9 **L**	May 9 **L**
40	16	Plantago lanceolata ♂	12 **L**	—	9 **L**
41	16	Geranium Robertianum	12 **L**	May 10 **L**	—
42	16	Chelidonium majus	—	—	—
43	17	Ranunculus acris	May 16 **L**	May 13 **L**	May 16 **L**

Table II—*continued.*

No.	1920	Name	1917	1918	1919
44	Apr. 19	Veronica montana	—	May 13 L	—
45	23	Cratægus oxycantha	—	1 L	May 18 L
46	23	Ranunculus repens (see Jan. 3)	—	10 L	15 L
47	24	Asperula odorata	May 15 L	17 L	24 L
48	24	Veronica hederæfolia	—	—	—
49	25	Ajuga reptans	May 7 L	Apr. 28 L	May 14 L
50	25	Viburnum lantana	—	—	—
51	25	Heracleum sphondylium	—	May 11 L	May 20 L
52	25	Anthoxanthum odoratum	—	9 L	15 L
53	25	Pyrus Aucuparia	—	—	19 L
54	28	Trifolium pratense	May 12 L	May 14 L	16 L
55	28	Orchis morio	23 L	—	15 L
56	28	Ranunculus bulbosus	—	Apr. 28 =	11 L
57	29	Allium ursinum	May 16 L	May 10 L	14 L
58	29	Alopecurus pratensis	—	9 L	17 L
59	29	Ranunculus aquaticus	—	—	12 L
60	30	Veronica serpyllifolia	—	May 9 L	15 L
61	May 2	Trifolium agrarium	—	17 L	18 L
62	3	Poterium sanguisorba ♂	Ju. 8 L	17 L	22 L
63	5	Sanicula europæa ♀	—	16 L	28 L
64	5	Scrophularia nodosa	Ju. 7 L	29 L	—
65	6	Acer campestre	—	5 E	May 24 L
66	6	Cardamine amara	—	—	26 L
67	12	Geum urbanum	May 28 L	May 14 L	21 L
68	12	Geranium molle	—	—	—
69	13	Rhinanthus Crista-galli	May 31 L	May 20 L	Ju. 5 L
70	13	Polygala vulgaris	Ju. 12 L	21 L	May 25 L
71	13	Chrysanthemum leucanthemum	May 30 L	22 L	28 L
72	14	Ilex Aquifolium	—	—	—
73	15	Bunium denudatum	—	—	May 20 L
74	16	Sonchus oleraceus	Ju. 21 L	—	Ju. 24 L
75	16	Trifolium procumbens	—	—	—
76	17	Lychnis Flos-cuculi	May 31 L	May 18 L	May 25 L
77	17	Veronica Beccabunga	29 L	17 =	26 L
78	19	Rubus cæsius	28 L	21 L	28 L
79	19	Sonchus arvensis	—	—	—
80	20	Orchis maculata	Ju. 11 L	May 24[1] L	Ju. 2 L
81	20	Potentilla Tormentilla	25 L	Ju. 10 L	May 27 L
82	20	Sanicula europæa	—	May 16 E	28 L
83	22	Parietaria officinalis ♀ stage	July 12 L	July 6[2] L	July 8[2] L
84	22	Anthriscus Cerefolium	—	—	May 23 L
85	23	Bryonia dioica	Ju. 9 L	May 30 L	♂ 28 L
86	23	Euphrasia officinalis	Aug. 3 L	—	July 28 L
87	23	Hypochæris radicata	—	May 27 L	May 29 L
88	24	Rosa canina	—	21 E	Ju. 6 L
89	25	Chærophyllum temulum	—	29 L	1 L
90	25	Evonymus europæus	Ju. 6 L	17 E	May 28 L
91	26	Cornus sanguinea	6 L	Ju. 2 L	Ju. 10 L
92	26	Sambucus nigra	10 L	May 21 E	May 29 L
93	26	Orchis latifolia	25 L	24 E	—
94	27	Ægopodium Podagraria	—	Ju. 6 L	Ju. 7 L
95	27	Parietaria officinalis ♂ stage	July 12 L	July 6 L	8[2] L

[1] Leaves not spotted. [2] No sex given.

Table II—*continued.*

No.	1920	Name	1917	1918	1919
96	May 27	Tamus communis	Ju. 6 **L**	May 28 **L**	Ju. 2 **L**
97	27	Sherardia arvensis	—	10 **E**	—
98	27	Lotus corniculatus	—	22 **E**	May 18 **E**
99	27	Lychnis vespertina	—	29 **L**	Ju. 8 **L**
100	27	Ranunculus arvensis	Ju. 3 **L**	—	24 **L**
101	27	Solanum Dulcamara	6 **L**	May 27 =	6 **L**
102	27	Onobrychis sativa	July 3 **L**	Ju. 6 **L**	2 **L**
103	27	Trifolium repens	Ju. 13 **L**	8 **L**	8 **L**
104	27	Hieracium pilosella	—	10	2
105	28	Galium aparine	Ju. 4 **L**	May 23 **E**	May 28 =
106	28	Scrophularia aquatica	—	—	—
107	28	Poa pratensis	—	—	—
108	28	Linaria cymbalaria (average)	Ju. 12 **L**	May 16 **E**	May 18 **E**
109	28	Lolium perenne	—	Ju. 10 **L**	Ju. 13 **L**
110	29	Potentilla reptans	Ju. 18 **L**	13 **L**	10 **L**
111	29	Potentilla anserina	—	May 27 **E**	4 **L**
112	29	Œnanthe crocata	Ju. 18 **L**	—	13 **L**
113	29	Rumex acetosa	♂My 29 =	May 21 **E**	♂My 25 **E**
114	29	Urtica dioica ♂ (average)	♂Ju. 5 **L**	25 **E**	♂ Ju. 2 **L**
115	30	Linum catharticum	8 **L**	25 **E**	6 **L**
116	30	Stachys sylvatica	May 30 =	Ju. 2 **L**	6 **L**
117	31	Helianthemum vulgare	Ju. 12 **L**	4 **L**	2 **L**
118	31	Avena pratensis	—	May 29 **E**	2 **L**
119	31	Rumex aquaticus (?)	—	—	—
121	Ju. 1	Neottia Nidus-avis	—	—	—
122	1	Plantago media	Ju. 6 **L**	May 22 **E**	Ju. 2 **L**
123	1	Tragopogon pratense	—	—	8 **L**
124	1	Milium effusum	—	—	May 27 **E**
125	2	Bromus arvensis	—	—	26 **E**
126	3	Dactylis glomerata	Ju. 10 **L**	Ju. 3 =	Ju. 1 **E**
127	3	Genista tinctoria	14 **L**	11 **L**	9 **L**
128	3	Briza media	11 **L**	6 **L**	6 **L**
129	5	Listera ovata	12 **L**	—	—
130	5	Polygonum aviculare	—	—	July 24 **L**
131	5	Rosa arvensis	May 21 **E**	—	7 **L**
132	5	Epilobium montanum	Ju. 12 **L**	May 28 **E**	Ju. 3 **E**
133	6	Ophrys apifera	July 11 **L**	July 16 **L**	—
134	6	Rubus fruticosus, var. glandulosus	—	—	Ju. 7 **L**
135	8	Spiræa ulmaria	Ju. 17 **L**	Ju. 5 **E**	Ju. 22 **L**
136	8	Lathyrus pratensis	8 =	17 **L**	12 **L**
137	8	Lapsana communis	18 **L**	16 **L**	20 **L**
138	8	Arrhenatherum avenaceum	—	—	8 =
139	9	Galium cruciatum (gathered 11th in *full* flower)	—	—	—
140	11	Ophrys muscifera	—	—	—
141	11	Carduus palustris	Ju. 14 **L**	May 31 **E**	Ju. 9 **E**
142	12	Lonicera Periclymenum	—	—	21 **L**
143	12	Rubus fruticosus	Ju. 22 **L**	Ju. 24 **L**	July 10 **E**
144	13	Cephalanthera	—	—	—
145	13	Orchis pyramidalis	Ju. 21 **L**	Ju. 13 =	Ju. 22 **L**
146	13	Carduus acaulis	July 7 **L**	July 8 **L**	July 4 **L**

Table II—*continued.*

No.	1920	Name	1917	1918	1919
147	Ju. 13	Reseda luteola	July 27 L	—	Ju. 26 L
148	13	Thymus Serpyllum	Ju. 12 E	Ju. 24 L	Ju. 30 L
149	13	Sedum acre	—	—	—
150	14	Ligustrum vulgare	—	—	—
151	14	Lonicera Xylosteum	—	—	—
152	16	Centaurea nigra	Ju. 17 L	Ju. 6 E	Ju. 19 L
153	16	Cynosurus cristatus	—	13 E	—
154	16	Pimpinella Saxifraga, var. β dissectifolia	—	—	—
155	17	Papaver Rhœas	Ju. 21 L	July 2 L	Ju. 21 L
156	18	Lactuca muralis	—	—	Ju. 23 L
157	19	Herminium Monorchis	—	Ju. 12 E	—
158	20	Geranium molle	—	—	—
159	20	Scabiosa arvensis	July 1 L	—	Ju. 25 L
160	20	Malva moschata	Ju. 21 L	Ju. 29 L	21 L
161	20	Geranium pratense	—	—	25 L
162	20	Circæa lutetiana	July 26 L	Ju. 17 E	22 L
163	20	Carduus nutans	—	—	—
164	21	Hypericum hirsutum	Ju. 27 L	Ju. 20 E	Ju. 23 L
165	21	Silaus pratensis	—	—	—
166	21	Campanula glomerata	Aug. 21 L	Ju. 19 E	—
167	22	Agrimonia Eupatoria	Ju. 27 L	—	Ju. 27 L
168	22	Vicia tetrasperma	—	—	—
169	22	Holcus lanatus	—	Ju. 16 E	—
170	22	Hordeum pratense	—	July 2 L	Ju. 22 =
171	22	Ranunculus sceleratus	—	Ju. 20 E	—
172	22	Anagallis arvensis	—	July 2 L	July 8 L
173	22	Matricaria Chamomilla	Ju. 12 E	10 L	Ju. 22 =
174	23	Scabiosa Columbaria	July 7 L	July 16 L	July 13 L
175	23	Verbascum nigrum	7 L	—	13 L
176	23	Centaurea scabiosa	Ju. 21 E	Ju. 29 L	Ju. 21 E
177	24	Medicago sativa (?)	—	—	July 12 L
178	25	Plantago major	July 13 L	July 5 L	Ju. 20 E
179	25	Campanula Trachelium	17 L	11 L	July 13 L
180	25	Asperula cynanchica	—	—	Ju. 30
181	25	Epilobium parviflorum	—	Ju. 30 L	July 10 L
182	27	Lysimachia Nummularia	July 5 L	July 7 L	2 L
183	27	Achillea Millefolium	7 L	5 L	Ju. 26 E
184	28	Chlora perfoliata	—	—	—
185	28	Valeriana officinalis	—	—	—
186	29	Carduus arvensis	Ju. 27 E	Ju. 30 L	Ju. 27 E
187	29	Æthusa cynapium	July 17 L	July 2 L	July 12 L
188	30	Aira cæspitosa	—	—	—
189	30	Glyceria fluitans	—	—	—
190	30	Galium verum	Ju. 21 E	Ju. 29 E	Ju. 21 E
191	30	Vicia cracca	—	July 7 L	—
192	July 1	Agropyrum caninum	—	10 L	—
193	3	Hypericum perforatum	—	9 L	—
194	3	Tilia	July 2 E	Ju. 30 E	July 9 L
195	4	Pyrola minor			
196	4	Epilobium hirsutum	—	July 6 L	6 L
197	4	Convolvulus arvensis	Ju. 18 E	2 E	Ju. 22 E
198	4	Bartsia Odontites	July 17 L	12 L	July 11 L
199	5	Hypericum hirsutum	Ju. 27 E	Ju. 20 E	Ju. 23 E

Table II—*continued.*

No.	1920	Name	1917	1918	1919
200	July 5	Apium nodiflorum = Helosciadium nodiflorum	—	July 7 L	July 14 L
201	5	Œnanthe pimpinelloides	—	—	—
202	6	Convolvulus sepium	Ju. 27	July 11	July 4
203	6	Ballota nigra	—	—	—
204	7	Scabiosa succisa	—	—	—
205	7	Scabiosa arvensis	July 1	—	Aug. 17
206	8	Sedum album	11	July 1	—
207	9	Digraphis arundinacea	—	6	Ju. 24
208	10	Carduus acanthoides	—	11	—
209	10	Brachypodium pinnatum	—	Ju. 24	Aug. 9
210	11	Habeneria viridis[1]	Aug. 11	—	July 28
211	11	Senecio Jacobœa	July 11	July 14	15
212	12	Anthemis arvensis	—	2	23
213	14	Agrostis alba	—	—	24
214	14	Hypericum hirsutum (not pale form)	Ju. 27	—	—
215	16	Bromus asper	—	July 16	July 22
216	16	Ononis spinosa	—	—	4
217	18	Campanula rotundifolia	July 6	July 9	—
218	19	Helminthia echioides	—	—	—
219	19	Epilobium tetragonum	—	—	—
220	21	Origanum vulgare	July 17	July 16	July 13
221	21	Clematis Vitalba	10	10	12
222	21	Veronica Buxbaumii	—	—	Apr. 22
223	24	Arctium Lappa	July 19	—	July 20
224	24	Stachys Betonica	11	July 13	18
225	28	Inula Conyza	Aug. 3	—	27
226	29	Eupatorium cannabinum	19	July 13	23
S 227	Aug. 4	Rumex Acetosella	—	—	—
S 228	4	Calluna vulgaris	—	—	—
S 229	5	Artemisia vulgaris	—	—	—
230	6	Lycopsis arvensis	—	—	—
S 231	6	Linaria vulgaris	—	—	—
S 232	6	Ulex europæa	—	—	—
S 233	6	Erica cinerea	—	—	—
S 234	7	Hypericum humifusum	—	—	—
S 235	7	Teucrium scorodonium	—	—	—
S 236	7	Potentilla argentea	—	—	—
S 237	7	Spergularia rubra	—	—	—
S 238	7	Cuscuta europæa	—	—	—
S 239	8	Corydalis claviculata	—	—	—
S 240	9	Ornithopus perpusillus	—	—	—
S 241	10	Erodium cicutarium	—	—	—
S 242	10	Viola tricolor	—	—	May 10
S 243	10	Antirrhinum Orontium	—	—	—
S 244	11	Jasione montana	—	—	—
S 245	11	Trifolium arvense	—	—	—
S 246	11	Bartsia odontites	July 17	July 12	July 11
S 247	12	Solidago Virga-aurea	—	—	—
S 248	12	Hypericum perforatum	—	July 9	—
S 249	14	Galeopsis tetrahit	—	11	—
S 250	14	Ballota nigra	—	—	—

[1] Found July 11 in advanced condition.

Table II—*continued.*

No.	1920	Name	1917	1918	1919
S 251	Aug. 16	Daucus Carota	July 11	July 12	July 18
S 252	17	Lamium amplexicaule	—	—	—
S 253	17	Fumaria officinalis	—	—	—
S 254	17	Sedum Telephium	—	—	—
S 255	17	Senecio sylvaticus[1]	—	—	—
S 256	19	Polygonum convolvulus	—	—	—
C 257	21	Calamintha menthifolia	—	—	—
C 258	23	Delphinium consolida	—	—	—
C 259	24	Humulus lupulus (? wild)	—	—	—
C 260	24	Lycopus europæus	—	—	—
C 261	24	Solanum nigrum	—	—	—
C 262	24	Sagittaria sagittifolia	—	—	—
C 263	24	Lycium barbarum	—	—	—
C 264	27	Stachys palustris	—	—	—
C 265	27	Inula dysenterica	—	—	July 23
C 266	28	Lychnis Githago	—	—	—
C 267	28	Lythrum salicaria	—	—	—
C 268	28	Mentha sativa	—	—	—
C 269	28	Selinum carvifolia	—	—	—
270	31	Scabiosa succisa	—	—	Aug. 17
271	Sep. 1	Sison amomum	—	—	July 28
C 272	2	Gentiana Amarella	Aug. 20	—	Aug. 28

[1] No. 259 should perhaps have been noted on a slightly earlier date.

The letters L and E in Table II show (as above stated) the broad relations between the dates of 1920 and those of 1917, 1918 and 1919. The letter L means that the species so marked flowered later than in 1920; in the same way E indicates earlier flowering.

What is at once obvious is that the 1917 dates are universally later than the corresponding entries for 1920. The same thing is, roughly, true of 1919, there being only three cases in the first 100 which are earlier than 1920, and one plant flowered on the same day in 1919 and 1920. In 1918 the case is different. Taking the same material, viz. No. 7 to No. 107, we have:

March 3–April 11	12 E	11 L	
April 13–May 13	1 E	21 L	2 equal
May 14–May 27	8 E	18 L	2 equal
The sums are...	21 E	50 L	4 equal

We see that the cases in which the spring flowers of 1918 (March 3–May 27) were earlier than those of 1920 are 21 in number: the cases in which 1918 is later being 50; there are also four cases

of equality. Thus out of a total of 75 cases 28 per cent. are early, 67 per cent. late and 5 per cent. are equal.

It should be noted that among the early cases a majority occurs between March 3 and April 11.

In conclusion, it may be pointed out that there is a general resemblance between 1920 and 1918, inasmuch as the springtime flowerings are early in both these years. And this fact we must connect with the relatively high temperatures ruling in the spring of these two years. Thus from the week ending Jan. 26, 1918, to week ending Feb. 16 we have deviations from the normal of + 6·2 to + 9·8. And, again, from March 16 to April 13 the deviations are + though not so well marked as those quoted.

The early spring flowerings of 1920 also correspond with the relatively high temperatures ruling from the week ending Jan. 10, 1920, to that ending Feb. 21, 1920.

THE THEORY OF GEOTROPIC RESPONSE

By V. H. BLACKMAN

In recent numbers of this journal (**19**, pp. 49–63 and 208–212) Professor Small has put forward a theory to explain the geotropic response in plants, and particularly the difference in the behaviour of the stem and the root. This theory rejects the movement of comparatively large cell particles (such as starch grains) as the first step in the chain of processes which lead to geotropic curvature, and relates the response to changes in the plasma itself under the action of gravity. The particles or drops forming the disperse phase of the colloidal protoplasm are supposed to be lighter than the surrounding fluid (continuous phase) and to rise to a marked extent under the action of gravity, a phenomenon which is described as "creaming." As these particles are electrically charged their movement should produce a difference of potential or alter the difference of potential already existing in the cell. The particles are supposed to be electro-positive in the root and electro-negative in the stem; the differences of potential produced, and the electric currents to which they give rise, would thus be in opposite directions in the two organs. These currents are supposed to affect the permeability and growth of the cells and so bring about the geotropic curvature.

The nature of the geotropic response (even if the statolith theory be accepted) is one of the most obscure of physiological phenomena,

especially in the diversity of reaction of the stem and the root. Professor Small has therefore shown great courage in attacking the problem and great ingenuity in working out his theory. Our knowledge of the colloidal and electrical conditions of the living cell is unfortunately so slight that any theory of this kind must be highly speculative, but in considering the theory as a working hypothesis a number of serious difficulties appear to arise, some of which are here put forward.

(1) One difficulty—and it is naturally a fundamental one—is as to the actual occurrence of the "creaming" effect. As is well known, there is no obvious settling of colloidal solutions; gold solutions made by Faraday more than sixty years ago are still to be seen at the Royal Institution. Yet, on the other hand, far smaller particles, for example, gaseous molecules, do settle to some extent as is clearly shown by the decrease in air pressure as we rise above sea-level. The explanation of this apparent discrepancy is that all particles settle to some degree, whether they are gaseous, molecules, ultra-microscopic particles, or microscopic particles; but the degree to which they settle (*i.e.* the alteration of concentration with height) depends on the volume of the particles and their relative density. The atmosphere follows what is called the exponential "rarefaction law"; if we go up six kilometres the density (*i.e.* concentration of molecules) falls to one-half, if we go up another six kilometres it falls to one-quarter, and so on. Einstein in 1905, and independently Perrin in 1908, showed that if the Brownian movement of particles is due to molecular bombardment the distribution with height of such particles must follow the same law. The amount of settling or rising for any given height—whether the particles are gaseous molecules or colloidal particles—will depend on the volume of the molecules or particles and their density. Perrin[1] was able to demonstrate by examination of carefully prepared colloidal solutions of gamboge and mastic that the particles did obey the "rarefaction law," for at each equal step upwards the concentration of particles decreased in geometrical progression. Perrin, in one of his experiments, found that for gamboge particles of radius $0{\cdot}21\,\mu$ the concentration was halved for each rise in height of $30\,\mu$.

From data such as these of Perrin's we can obtain some idea of the degree of settling or "creaming" which would result from the action of gravity on the colloidal particles of the protoplasm. Perrin worked with microscopic particles; the protoplasmic

[1] J. Perrin, *Brownian Movement and Molecular Reality.* (English translation), London, 1910; also *Atoms* (English translation), London, 1916.

ones in question are ultra-microscopic, and we may assume their diameter to be 1/10th that of Perrin's gamboge particles—an assumption which does not seem to err on the side of smallness. The relative density may be assumed to be the same as the gamboge particles (0·207), though that of the protein drops of the cell would probably be less. As the volume of the particles is only 1/1000th that of the gamboge ones, it would require a cell 30 *millimetres* high to obtain a difference of concentration of 50 per cent. between the top and bottom. Taking a meristematic cell of the root as 30 μ across, it is easy to calculate that for ultra-microscopic particles of the size suggested the drop in concentration between the top and bottom of the cell would be only 7 parts in 10,000, or 0·07 per cent.; if the cell is taken as 50 μ broad it is still only 11 parts in 10,000, or 0·11 per cent.[1] There is thus no reason to believe that the differences of concentration of particles in the cell produced under the action of gravity would be other than negligible in amount, and in fact so small that the term "creaming" can hardly be applied. It seems inconceivable that such small differences in concentration could produce the marked electrical effects required by Professor Small's theory.

(2) There is another great difficulty which the theory presents, namely, that of the factor of time. It is easy to show that even the very small movement—which, as pointed out above, is all that can be expected of the cell particles—would take place so slowly that it could not be a link in the chain of processes which controls the rapid geotropic reaction of the stem and root. Perrin, working with the large colloidal particles of radius 0·21 μ, allowed three hours for the completion of the process. With decrease in size of the particles or increase in viscosity of the medium, however, the time taken to reach equilibrium increases. In another of Perrin's experiments with rather larger particles (0·38 μ radius) and a highly viscous medium (viscosity 125 times that of water) the time taken to reach equilibrium was "several days." One can calculate from this that particles no smaller than of 0·034 μ radius moving in a watery medium would also take days to reach equilibrium. As by the author's hypothesis the particles are ultra-microscopic and so must be of this order of size and probably smaller, and the cell medium in which they move is more viscous than water and possibly highly viscous, *the time taken to settle down or rise up under the action of gravity must also be of the order of days.*

[1] Even if the diameter of the ultra-microscopic particles of the protoplasm be taken as only 1/5th of that of the gamboge particles, the difference in concentration in cells 30 μ and 50 μ broad would be only 0·6 per cent. and 0·9 per cent. respectively.

Professor Small refers to Perrin's work on Brownian movement (1910, *loc. cit.*) in which it was demonstrated that the rate of fall or rise of colloidal particles under the action of gravity can be calculated from Stokes' law. The conclusion, however, he draws from Perrin's work that in the cell the "creaming is governed by Stokes' law" (footnote, p. 52) is certainly mistaken. Once it is recognised that colloidal particles obey the "rarefaction law" it is obvious that Stokes' law, which applies to freely falling particles, is only followed when the particles are far removed from their equilibrium distribution. Perrin makes this point clear (*loc. cit.* 1910, p. 34), and in investigating the application of this law to the comparatively large particles of gamboge he used a tube several cms. long. The small ultra-microscopic granules within the narrow confines of a cell only 0·05 mm. in height must always be little removed from their limiting distribution, as demonstrated above; they therefore cannot fall freely and Stokes' law cannot apply. In order that the plasma particles should be under the same conditions as Perrin's gamboge particles a cell at least a *metre* high would be required[1].

The considerations put forward above indicate that any rearrangement of the cell particles which might occur under the action of gravity would be exceedingly small in amount, and would be accomplished very slowly. The geotropic response, on the other hand, is a particularly rapid process. Under ordinary conditions a "presentation time" as low as two minutes has been observed, and the "excitation time" is certainly very much less. Professor Small has himself described earlier a geotropic reaction appearing as a change in electrical conductivity of the cells of the root tip which is to be observed in as short a period as 20 seconds after the organ is placed horizontal. Bose (*Trans. Bose Inst.* II, pp. 500 and 452, 1919) found in one case a large electric response occurring one second after the horizontal position was reached, and in another case the maximum deflection was attained in 90 seconds. It would seem impossible to correlate active electrical and mechanical reaction occurring in a few seconds or minutes with a redistribution of plasma particles so limited in extent and requiring days for its accomplishment.

(3) There is also another difficulty which would seem to arise if

[1] Even if the cell particles were able to move freely, their small size would render their rate of rise, as calculated by Stokes' law, very low. If we assume that their radius is 0·021 μ and that their relative density is the same as Perrin's gamboge particles (*i.e.* 0·207), and that the viscosity of the protoplasmic medium in which they move is only twice that of water (0·01), the rate of ascent would be only 1 μ in 10,000 secs. = 2·8 hours. The rate would really be slower as the particles by their movement are doing work in producing a difference of potential in the cell.

the "creaming" occurred and a difference of potential were produced. Since the potential, which is assumed to result from the movement of the particles, is, *ex hypothesi*, being dissipated by the current which it produces in the organ, it should soon disappear when the "creaming" is complete. In an organ kept horizontal it would seem that the difference of potential produced by the "creaming" should soon cease to exist, and, as the current produced by this difference is by the theory the cause of the curvature, the organ should soon cease to react to gravity. A root compelled to grow for a time through a short horizontal tube should, on becoming free at the other end, have lost the power of geotropic response. The same difficulty arises as to the origin of the currents in the axial and lateral organs, which, Professor Small holds (*loc. cit.* pp. 59 and 209), explain the relation of secondary branches to the primary root and stem. The normal polarisation of the plasma membrane will not produce currents in uninjured cells. Also the apical meristems of, for example, the normal undisturbed root system, would have been "creamed" from their first origin, so no difference of potential should arise in their case.

The recent experiments of Bose (*loc. cit.*) do seem definitely to support the statolith hypothesis in the case of the stems he examined. When the stem is horizontal, a high E.M.F. is rapidly attained; it is at its maximum when a lead is taken from the endodermis, and no current is obtained when the electrode is in the centre of the stem; also he found that when the starch grains had disappeared from the endodermis there was no electric response of the stem. Bose also described a striking case where there was no electric response when the flower stalk of *Nymphaea* was displaced by 33°, but "when this critical angle was exceeded by a single degree there was a sudden precipitation of geo-electric response" (p. 500). This would seem to be consistent with the sticking and displacement of large particles, but is quite inconsistent with the movement of ultra-microscopic ones in the protoplasm.

That the hydrogen-ion concentration of the protoplasm plays an important *rôle* in cell processes, and that differences in this respect may explain the difference of geotropic response of the root and stem as assumed by the theory, would seem very plausible. If, however, a reaction which takes place as rapidly as the geotropic response is to be correlated with the movement of particles in a viscous medium it would seem certain that such particles must be comparatively large and heavy, not ultra-microscopic.

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REVIEW

Practical Plant Biochemistry By Muriel Wheldale Onslow. (Cambridge University Press, 1920.) pp. i + 178. Price 15s.

The author, who is well known from her previous book, *The Anthocyan Pigments of Plants*, points out in the preface that the volume is compiled primarily for students of Botany who have some knowledge of Organic Chemistry. Its title might suggest that it is solely a laboratory manual, but, in fact, it combines in a very useful way a small text-book of plant chemistry with directions for numerous practical exercises. There are ten chapters, of which six deal with the chief classes of chemical compounds to be found in plants, namely, carbohydrates, fats and lipases, aromatic compounds and oxidising enzymes, proteins and proteases, glucosides and glucoside-splitting enzymes, and the plant bases, the last chapter being a very useful addition. There are, besides, an introductory chapter, and chapters on the colloidal state and on enzyme-action, and also a chapter on carbon-assimilation which includes a useful *résumé* of the chemistry of chlorophyll. Here and there we find a brief discussion of a few physiological problems such as those of the first formed sugar of the green leaf, and of the synthesis of fats, and a short but useful list of references is appended to each chapter. It is satisfactory to find in the chapter on carbohydrates a short account of the pentosans, the importance of which in succulent plants is being more and more recognised. In this chapter, however, mention might have been made of all the sugars which are referred to later in connexion with the splitting of glucosides. The statement, also, that "all these structural elements [of the plant] can be translated into terms of chemical compounds" seems to savour more of expectation than of present-day realisation. The colloidal state and enzyme-action are somewhat cavalierly treated and the references to surface action are almost too brief to be helpful; these two chapters might usefully be expanded in a later edition. These minor criticisms apart, the book is certainly a marked success, and the author is to be congratulated on an introduction to plant biochemistry which is interesting, clear and compact, and which for the first time makes the subject easily accessible to the average botanist. The practical instructions given should also help to improve in universities the quality of the laboratory work in plant biochemistry.

V. H. B.

THE ANGLO-AMERICAN UNIVERSITY LIBRARY FOR CENTRAL EUROPE

It is now well known that the scientific men of Central Europe are severely handicapped in their efforts to obtain scientific literature from foreign countries owing to their poverty and to the very unfavourable rates of currency exchange. An organisation has been formed to establish libraries for Central Europe from which books and papers are to be distributed to the university professors and teachers who require them. Eight centres of distribution have

at present been established: Berlin, Budapest, Frankfurt, Göttingen, Munich, Krakow, Prague and Vienna, and several consignments of literature have already been sent to these centres. The organisation for the United Kingdom is under the control of a strong committee under the presidency of Viscount Bryce and the chairmanship of Sir William Beveridge.

Gifts of separate copies of scientific papers which have appeared since 1914, as well as spare copies of books and periodicals, would be very useful, and should be sent to the Hon. Secretary, Mr B. M. Headicar, London School of Economics, Clare Market, London, W.C. 2, by whom they will be gratefully acknowledged. Cheques and money orders to help the scheme should be sent to Lieut.-Col. George Schuster, at the same address.

We appeal to our readers and contributors to do what they can in aid of this admirable scheme of help to our fellow-workers in Central Europe.

THE BRITISH COMMITTEE FOR AIDING MEN OF LETTERS AND SCIENCE IN RUSSIA

A STRONG committee of British men of science and letters, including the President of the Royal Society, the Editor of *Nature*, Mr Ernest Barker, *et al.*, has been formed to help Russian men of science and letters, who are suffering great privations and have had practically no access to European literature since the Revolution. Some members of the British committee have recently been in direct communication with the Russians, and a comprehensive list of books and other publications, which they most urgently need, has been made. The purchase of these and the cost of transmission will involve a considerable expenditure, and the British committee are asking for subscriptions, which should be sent to the Treasurer, Dr C. Hagberg Wright, British Science Guild Offices, 6, John Street, Adelphi, London, W.C. 2.

It is understood that there will be no obstacle to the transmission of the literature to the House of Science and the House of Literature and Art in Petrograd, the present headquarters of the Russian savants. This scheme also we cordially commend to those of our readers who can afford financial help.

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THE NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL

EDITED BY

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IN CONSULTATION WITH THE STAFF OF
THE CAMBRIDGE BOTANY SCHOOL

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THE
NEW PHYTOLOGIST

VOL. XX, No. 2 JUNE 30, 1921

PERMEABILITY

By WALTER STILES

CHAPTER I

INTRODUCTION

IN the study of the living organism there presents itself a well marked group of problems arising from phenomena which can be included under the term "Permeability." Every organism receives from its environment in some form or another substances which enter into its body and which either as such, or after undergoing physical and chemical change and working up into new combinations, may be carried to every part of the organism. The problems concerned in this intake into the organism of substances from the surroundings, and their passage out from the cell into the external medium, and the translocation of substances from cell to cell in the body of the organism, may be spoken of broadly as problems of permeability. It must be admitted at the outset that the word permeability in biology is largely a cloak for ignorance. When the physical chemist speaks of the permeability of a membrane, he refers to the capacity of the membrane for allowing substances to pass through it, and this is the logical and correct significance of the term. But this is not always what is meant when the physiologist speaks of the permeability of protoplasm or the permeability of an organic cell. Sometimes he means the capacity of a substance to pass into or out from the cell, sometimes its capacity to pass through one particular part of the cell, as, for instance, the protoplasm, or the surface layer of it. The cell is a complex structure, and in the present state of our analysis it is rarely possible to localise the seat of any cellular phenomena exactly, although it must be one

of the objects of research to do so. While therefore we must aim at a stricter use of the term permeability so as to conform to its usage in physical chemistry, at present our knowledge simply does not allow us to do so when we are dealing with the problems of the cell.

Research on the problems involved has proceeded along two rather distinct lines. In one, the whole living organism has been the unit of experimentation, while in the other isolated cells and tissues have been employed. In the case of unicellular and other small organisms the difference between the two groups of methods disappears. The difference between the two lines of attack is, however, very obvious in the case of work on higher plants where the methods of the first mode of attack are for the most part those of pot culture and water culture. In the hands of a number of plant physiologists from Woodward in 1699 onwards, research by these methods led to fundamentally important discoveries in regard to plant nutrition, and in the hands of Sachs and Knop about 1860 it was used to demonstrate successfully the elements essential for the nutrition and development of plants, the absorption of water and dissolved substances from the soil and the absorption of gases from, and their excretion into, the air. The methods as employed to-day have provided a quantity of empirical information on the relation between the amount of growth of plants and the constitution of the medium external to their roots; as far as permeability problems are concerned they have not led us much further than the experiments of Sachs, Knop and other workers of their time, who showed by water-culture experiments that plants were capable of absorbing certain substances through their roots, while ash analyses showed that the constituents of these substances were capable of passing through the tissues to remote parts of the organism. These methods, in short, afford no data in regard to the intake of salts by the plant and the subsequent movement of the absorbed substances, beyond the information that these take place in certain cases. Nevertheless in the past they yielded results of the first importance for our subject, and there is no reason to suppose that, with suitable modification, their period of usefulness is over.

In the animal organism similar considerations hold. From considerations based on the whole organism as a unit it early became clear that some substances could penetrate through certain cells and become absorbed into the animal, while others could not. But, generally speaking, this line of attack has not afforded quantitative

data bearing on permeability, and so has not greatly helped towards a clear insight into the problems involved.

It is to the second line of attack that we owe most of our knowledge of permeability. The use of isolated cells or isolated pieces of tissue allows the employment of more exact methods and more careful control than can always be obtained in experiments with the whole organism. Such material as roots or stems and slices of storage tissues such as tubers or fleshy roots in the case of plants, blood corpuscles, eyes, pieces of muscle in the case of animals, have formed successful objects of experimentation. The elimination of error arising from variability among different individuals, the so-called "biological error," is possible with this mode of attack, and by a proper method of experimentation results can be obtained approximating in exactness more nearly to those of physics and chemistry than is possible when whole plants or animals form the experimental object, and such results are reproducible.

As tissues differ in the form of the cells which compose them so they differ also in their functions, and it is reasonable to suppose there is no more uniformity in regard to permeability than in regard to other functions. By the use of isolated tissues we are thus on the way towards a physiological analysis which is not possible when the whole organism forms the experimental unit.

The problems of permeability are problems of general physiology; they are common to all life, plants and animals, the lowest and the highest. They are problems of the cell and of the organism as a whole. While in this account of our present knowledge of permeability we shall deal mainly with plants, we shall thus have occasionally to refer to work on animals, as this may often be helpful in understanding the conditions in plants, while the results of investigations dealing with plants from very different groups of the plant kingdom and with both whole plants and parts of plants will have to be considered.

CHAPTER II

THE SYSTEM INVOLVED

THE problem with which we are presented is then to discover the laws governing the penetration of substances into and through the living cell. It is obvious that it is of first importance to understand the system involved. Both from a chemical and physico-chemical point of view this is a very difficult matter. The essential of all living cells is protoplasm. The structure of this and its elementary properties have been described as among the most difficult problems with which the biologist has to deal (Bayliss, 1915). In its simplest form in Amoeba or Myxomycetes, the general body of the protoplasm, that is, the cytoplasm apart from enclosed granules, appears as a clear viscous fluid, apparently structureless, capable of changing its form under the influence of external conditions, but remaining quite distinct from, and without any tendency to mix with, the medium external to it.

It has been urged that protoplasm behaves as a liquid (Bayliss, 1915). This is shown by (1) the fact that drops of water enclosed in it assume a spherical form, (2) Brownian movement[1] observed by R. Brown in 1827 (R. Brown, 1866), (3) the action of an electric shock under the influence of which, an amoeba, for instance, tends to form a sphere (Kühne, 1864), (4) the behaviour of Myxomycetes (Lister, 1888).

Under ordinary powers of the microscope certain parts of the protoplasm are visible as denser specialised organs of the cell: the nucleus, numerous small granules, and in plants the plastids. Apart from these, under the ultra-microscope (dark-ground illumination) the apparently homogeneous cytoplasm is observed not to be homogeneous, but to contain a great number of minute particles (Gaidukov, 1906–1910; Mott, 1912; Price, 1914). This is the condition characteristic of colloidal solutions, and from ultra-microscopic observation it would seem reasonable to conclude that the cytoplasm is frequently a colloidal liquid system or hydrosol.

Cytoplasm then is not homogeneous, but consists of a denser phase dispersed through the watery dispersion medium. It thus

[1] Brownian movement of particles visible under the ordinary microscope cannot be observed in all cells or organisms (Seifriz, 1920).

has a structure, but it must be emphasized that this structure is ultra-microscopic and not coarse enough to be observed under the ordinary microscope as was at one time thought. The production of a reticulate structure in the cytoplasm when treated with fixing and staining agents led to the view that cytoplasm possessed a net structure visible under the microscope. Even if the views of some earlier writers more or less dimly suggest the opinion that cytoplasm is in the colloidal condition, and while Bütschli (1892) suggested that living protoplasm has the structure of a microscopic emulsion, it was Hardy (1899) and A. Fischer (1899) who showed that the structure of cytoplasm after treatment with fixing agents could be made to vary according to the treatment during fixation. The conclusion to be drawn is obviously that the reticulum generally observed is the result of the fixing, and for the reasons already given it must be held as undoubtedly true that cytoplasm is essentially a colloidal system.

Although in many cases the body of the cytoplasm is a sol, there is a certain amount of evidence that in many cells the cytoplasm may be in the more solid gel condition. Thus Bayliss (1919) says: "That there are possibilities of the formation of membranes, doubtless of a gel nature, within the protoplasm of a cell is shown by the fact that different reactions can take place at the same time in different parts of the cell, notwithstanding the general liquid nature of its contents." Gaidukov (1910) and Price (1914) by ultra-microscopic observation find that in some cases Brownian movement in the cell may cease, and suppose the protoplasm in these cases has taken on the state of a gel.

Price concludes that protoplasm can, and often does, exist in the gel state, and in this state may be active. Bayliss has been able to bring about the cessation of Brownian movement by weak electrical stimulation and relates the phenomenon with functional activity (1919). Chambers (1917), by microscopic observations made on dissections of living cells, also comes to the conclusion that in the ova of a number of marine organisms (*Asterias, Arbacia, Echinoarachnius, Cerebratulus, Fucus*) and in the germ cells of certain insects (*Periplaneta, Disosteira, Anasa*) as well as in protozoa, the cytoplasm usually exists as a sol. On the other hand he considers that in adult somatic cells, including nerve cells and muscle fibres, the protoplasm forms a more or less rigid gel. Leucocytes however possess a cytoplasm closely resembling that of germ cells. Seifriz (1918, 1920) also, in a similar series of observations on Myxomycetes,

oogonia, egg cells and embryos of *Fucus*, *Spirogyra*, *Vaucheria*, *Rhizopus* and *Zygorhynchus*, pollen tubes of *Iris versicolor*, *Lathyrus maritimus*, *Erythronium revolutum*, protozoa, and ova of *Echinoarachnius*, finds the viscosity of protoplasm varies greatly in the different cells examined. Young *Fucus* oogonia and embryos and the streaming protoplasm of Myxomycetes were the most liquid, the mature and resting eggs of marine organisms were the most viscous. This author however is of opinion (1920) that great caution should be exercised in using viscosity as the only criterion of a sol or gel condition of the protoplasm.

Price decides that in resting spores, for example, those of *Mucor*, the protoplasm is in the gel condition, but that on germination it becomes a sol. Changes in the consistency of *Fucus* eggs during maturation and fertilization are described by Seifriz (1918), while the same writer (1920) states that as a myxomycete prepares to fruit the protoplasm increases in viscosity until it becomes in consistency a gel. Seifriz has observed such changes in protoplasmic viscosity which are reversible. "The viscosity of protoplasm is not fixed, for it varies in different organisms, in the same organism at different times, and even in different regions of the same organism at the same time" (Seifriz, 1920).

Thus even where the bulk of the cytoplasm is a sol there is a considerable quantity of evidence that the surface layers of the cell plasm may be in the more solid gel condition. Loeb (1906) says confidently: "It is a general rule that every free cell is surrounded by a solid film." He instances as evidence of this the length of the pseudopodia of rhizopods, which is so great that if the pseudopodia were entirely liquid they would fall apart into droplets. As protoplasmic streaming takes place in the interior, the solid part of the pseudopodia must be at the surface. Ramsden (1894, 1903) and Traube (1867) have shown the formation of solid membranes at the surface of hydrosols.

In cells in which Chambers decides the cytoplasm is in the sol condition he finds the peripheral layer very dense in consistency as compared with the interior of the cell, the outer layer merging insensibly into the general body of the cytoplasm. This surface layer is particularly well marked in protozoa, for example, in *Paramoecium*. Chambers concludes that the surface layer is a "highly extensile contractile and viscous gel," which if damaged may be automatically repaired. In adult somatic cells where the interior cytoplasm is judged to be in the gel state it is not possible

to demonstrate an outer layer differing in consistency from the rest of the cell. Price from ultra-microscopic observations states that the presence of an outer layer of the protoplasm differentiated from the interior seems quite definite. In any case it must be emphasized that the surface of the cell constitutes a boundary between two immiscible phases and as such the properties of the surface will differ greatly from those of the main bulk of the protoplasm. Indeed, the surface layers of the protoplasm are generally regarded as differing so much from the rest of the protoplasm as to have different permeability properties. The evidence for and against this view will be more suitably dealt with in a later chapter when the cell membranes are considered in more detail.

The chemical composition of protoplasm is rendered difficult of determination as the methods of chemical analysis in themselves necessarily change the living matter into something essentially non-living and therefore different. Chemical analysis has however provided some information regarding the components of the living substance. Water often comprises about 80 or 90 per cent. of the total weight of protoplasm. The classical analysis of Reinke and Rodewald (1880) of the plasmodium of the myxomycete *Fuligo varians* showed that about 60 per cent. of the dry weight of the protoplasm consisted of proteins, about 20 per cent. of carbohydrates and fatty substances, while the remainder consisted of amino-acids and other organic acids, various organic bases and inorganic salts. In different samples of protoplasm the relative quantities of the substances of which it is composed vary; proteins may form as little as 40 per cent. of the total dry matter. It has been a matter of controversy whether cytoplasm is a single definite substance peculiar to living matter, or whether it is composed of a large number of relatively simpler substances. In the elaboration of the former view the molecule or "biogen" is held to consist of a stable central nucleus to which are attached side-chains capable of undergoing various chemical transformations such as oxidation and reduction, and to which the activities of the cell are due (Verworn, 1903). The opinion that protoplasm comprises a large number of different substances is more generally held to-day. Thus Czapek (1911) remarks: "But we have to concede that the chemical nature of protoplasm is not founded upon the peculiarities of one particular substance which is characteristic of living protoplasm. There are, we are certain of it, a great number of constituents of protoplasm which form the substratum of cell-life."

Hopkins (1913) thinks the biogen molecule theory "as inhibitory to productive thought as it is lacking in basis." Bayliss (1915) regards the biogen theory as "an example of the efforts of a certain school of physiologists to explain by purely chemical laws, such as mass action, facts which admit of a simpler explanation, if physical phenomena are also taken into account."

We have to think of protoplasm not merely as an intimate mixture of a large number of substances, but as having a complex organisation so that the cell is rather an organ with an intricate minute structure, and at the same time different reactions can take place in different parts of the same cell. "Protoplasm is an extraordinarily complex heterogeneous system of numerous phases and components, continually changing their relations under the influence of electrolytes and other agents" (Bayliss, 1919). For a further discussion of this question reference may be made to the writings of Verworn, Czapek, Hopkins and Bayliss cited above.

Some parts of the protoplasm are clearly differentiated from the rest. The most important of these is the nucleus which has been observed in all plant and animal cells with very few exceptions. From its appearance in fresh cells and from its reaction to stains it obviously differs from the cytoplasm that encloses it. There is considerable evidence that it is much richer in nucleoproteins, which contain phosphorus, than the surrounding cytoplasm. The observations of Gaidukov and Price with dark-ground illumination point to the fact that the nucleus is in the gel condition. Kite (1916) and Chambers (1917) conclude on the contrary that the resting nucleus of the ovum is in the sol state. Price made out a definite limiting layer separating the nucleus from the cytoplasm, but he thinks it possible that this, the so-called nuclear membrane, may be no more than the surface of separation between the cytoplasmic hydrosol and the nuclear hydrogel. The intimate connection between cytoplasm and nucleus as regards cell activity is so well realised that it needs no further emphasis.

The plastids occur only in plants, and even then not in all plants. They are absent, for example, from the Fungi. Like the nucleus they are sharply differentiated from the rest of the cytoplasm and appear to contain much protein. In addition they often contain pigments (chlorophyll, xanthophyll and carotin) our knowledge of the composition of which is due to the persistent researches of Willstätter (1913). According to Price the chloroplasts of *Spirogyra, Elodea* and other plants are, like the nucleus, in the gel state.

The small granules occurring throughout the cytoplasm may be in some cases tiny non-living inclusions and in other cases small plastids or other living bodies. Chemically they may be composed of fat, glycogen, protein, etc., as shown by microchemical tests. Chambers divides them into microsomes and macrosomes, the former being very minute and considerably less than 1 μ in diameter, while the macrosomes vary from 2 to 4 μ in diameter and are circular, oval or polygonal in shape. The macrosomes are the alveolar spheres of Wilson (1899), with whom Chambers disagrees as regards the complete gradation from macrosomes to microsomes. Chambers regards the two sets of bodies as quite distinct; the macrosomes are the most easily injured, and the microsomes are the most resistant, of all cell structures. Into this controversy we need not enter here, nor yet into the question to what extent the microsomes are identical with mitochondria. Those interested should consult the very numerous papers on this subject recently published by Guilliermond (1916–1921).

Whereas in animal cells the protoplasm frequently occupies the whole of the cell space, in plants this is the case only with meristematic cells. As the cell passes out of the meristematic condition small inclusions of less viscous consistency become obvious in the general mass of the cytoplasm. These are the vacuoles. As the cells grow older the vacuoles become larger and ultimately fuse into one large vacuole occupying the greater part of the cell cavity. Strands of cytoplasm traverse this vacuole and may even in the middle of the vacuole form a mass enclosing the nucleus. In the oldest cells which are still living even these strands may disappear and the cytoplasm is limited to a scarcely perceptible layer surrounding the vacuole. In this case the nucleus lies in this lining layer of cytoplasm; it is never in direct contact with the vacuole.

The contents of the vacuoles are very varied. Occasionally solid particles may occur, as for instance, those of calcium sulphate in certain Desmids. Such particles have been observed by G. S. West in a number of green algae (Price, 1914). Apart from these are particles of ultra-microscopic dimensions which have been observed by Price. Undoubtedly, however, as the facts of osmotic pressure and turgor show, the contents of the vacuole consist chiefly of an aqueous solution of various substances. Thus in the bulb of the onion and in the root of the beet the substance is mainly sugar (De Vries, 1884); in the bean, pea, buckwheat and maize it is said to be chiefly potassium nitrate (Copeland, 1897); in other plants

potassium chloride may be present in considerable quantity, while in many cases organic acids are the principal substances present (De Vries, 1879, 1883; Kraus, 1886).

At the junction of the vacuole and the cytoplasm we have again a surface separating two immiscible phases with consequently properties differing from those of either phase, and it has become usual to regard that part of the cytoplasm directly surrounding the vacuole as a distinct layer spoken of as the internal plasmatic membrane (Pfeffer, 1900) or the vacuole wall (De Vries, 1884). Price, by ultramicroscopic observation, has obtained indications of a definite layer in this location similar to that bounding the cytoplasm externally. To this question we shall have to return later.

Yet another complication is present in the case of plant cells, namely, the cell wall. Although this is absent in a few cases, nearly every plant cell is bounded by a firm envelope which thus separates the individual protoplasts from one another. The cell wall differs widely in morphological construction and chemical composition among different species and in different parts of the same plant, but with the exception of the Fungi one of the main constituents of the cell wall is cellulose, a carbohydrate, or more probably a group of carbohydrates, of high molecular weight. A number of other substances are present, these varying in different species and in different tissues of the same species. In the Fungi, including the Bacteria, the principal constituent of the cell wall is chitin. The cell wall of the young plant is always thin, but after the cell has reached its ultimate size, various morphological and chemical changes take place in the cell wall, for a description of which reference may be made to standard botanical text-books (for example, Sachs, 1875; Strasburger, 1903) and especially to the work of Mangin (1893). It should be mentioned here that thickening of the cell wall may consist entirely of cellulose and allied substances, or the walls may be modified by the processes of lignification, suberisation or cutinisation, in which various substances grouped under the names lignin, suberin and cutin (see Priestley, 1921) are deposited in the cell wall and profoundly alter its properties. It should also be observed that when cell walls become thickened the thickening is rarely uniform. Scattered over the cell walls places occur at which thickening does not take place so that thin spots known as pits are dotted over the surface. The pits on the two sides of a wall separating two cells are always opposite one another, so that at the pit there is only the original primary wall separating the two protoplasts. Chiefly through the

researches of W. Gardiner (1884), A. Meyer (1896), Strasburger (1901) and A. W. Hill (1901) it is clear that fine cytoplasmic threads penetrate the pit membranes, and sometimes indeed the whole thickness of the cell wall, so that in spite of the presence of the cell wall there is actually a continuation of protoplasm throughout the plant. Cellulose walls readily absorb water, and in the living plant the cell wall is normally permeated with imbibed water. Cutinised and suberised walls are however more or less impermeable to water, and their principal function is to prevent loss of water from the surface of cells.

Such then is the system with which we are concerned in a consideration of the problems of permeability. This system is very varied, attaining its highest complexity in the adult plant cell. In the latter we have to recognise at least three phases, the cell wall, the protoplasm and the vacuole. Each of these moreover is itself a complex system, both the cell wall and protoplasm each containing a more watery phase and at least one other phase, while there is evidence that the cell sap in the vacuole may also contain a colloidal disperse phase as well as water with substances in pure solution. At the boundaries between outer medium and cell wall, cell wall and protoplasm, protoplasm and vacuole, there are separating layers which there is every reason to believe have different properties from the bulk of the phases they separate. Further, in both the cell wall and protoplasm, and perhaps also in the vacuole, we have at least two-phase and probably polyphase systems in which there are consequently relatively large surfaces of contact between the phases. The constituents of the different phases vary from plant to plant and from tissue to tissue in the same plant.

We thus see how much phase boundaries figure in the structure of the cell, and it is impossible to lay too much stress on the importance that surface phenomena must play in regard to cell permeability. Before passing on to problems of the cell itself it will therefore be necessary to discuss briefly the more important facts relating to surfaces, as well as other physical and physico-chemical principles with which acquaintance is necessary for a proper realisation of permeability phenomena.

(*To be continued.*)

STOMATA AND HYDATHODES IN *CAMPANULA ROTUNDIFOLIA* L., AND THEIR RELATION TO ENVIRONMENT

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(With 6 figures in the text.)

Many authors have commented on the varying number of stomata observed either on the leaves of related plants, or on the leaves of plants belonging to widely differing families. Very little work so far has been done, by using the same species grown under different conditions, to demonstrate the possibility that the number of stomata per unit area may vary according to the leaf surface and the position of the leaf on the shoot. In this connection Professor R. H. Yapp found in *Spiraea Ulmaria* L. (= *Ulmaria palustris* Moench.) a range from about 300 to nearly 1300 stomata per sq. mm. on the under surface (there were practically no stomata on the upper surface) for the lower and upper leaves respectively of the same shoot (7, p. 827). He states: "It may be that *Spiraea Ulmaria* is exceptional in the latter respect, but it would be worth while comparing the successive leaves of a number of other plants, for if the phenomenon is at all general, the numbers already published for a large number of species might need considerable revision."

HISTORY.

Weiss (6, pp. 166–167) was one of the earliest workers who compared the numbers of stomata occurring in a large series of different plants. He found that members of the same family or even members of the same genus may show great differences in the number of stomata present, although the habitat, temperature and amount of moisture in the soil is the same (6, pp. 166–167). His conclusion is that habitat has no influence on the occurrence of the stomata. The halophytes, such as *Arenaria grandiflora* (6, pp. 123–132) and *Chenopodium ambrosioides*, had more stomata on the upper than the

under surfaces. This was also true of Conifers and Monocotyledons such as *Asphodelus luteus* and *Iris germanica*.

Tschirch at a later date reviewed the work of the earlier writers and quotes Morren as considering that "in related plants the number of stomata was in simple relation to the need for water." Czech (5, p. 169) considered that plants, of the same organization and family with varying numbers of stomata, can close them at will and so guard against over transpiration. Zingeler (5, p. 169), who worked with the Carices, found that those growing in a dry habitat had few stomata while those growing in a damp habitat had many. Tschirch (5, p. 173) concluded that on the whole plants in dry, stony places had fewer stomata than those growing in fields. In both habitats there were species with more stomata per sq. mm. on the upper than the under surfaces.

	Upper surface	Under surface	
Triticum sativum ...	47	32	Fields
Secale cereale ...	49	42	
Avena sativa ...	40	27	
Sedum album ...	49	25	Dry, stony places
Sedum acre	21	14	

But *Triticum* and *Avena* have more or less isobilateral leaves while the species examined from dry, stony places were succulents. Miss Delf (2, p. 501) records that the number of stomata on *Salicornia annua* increased the higher the internode, and that their size varied with the age of the internode, being smaller on the upper leaves. From the fact that, although there were many stomata present in *Salicornia annua*, there were few in *Suaeda maritima* and *Arenaria peploides*, she concludes that "the distribution of stomata in halophytes is a variable feature and throws but little light on the problem of transpiration in these plants." Yapp (7, pp. 826–828) found many more stomata per unit area on the upper leaves of *Spiraea Ulmaria* than on the lower leaves. He concluded that the larger numbers on the upper leaves were counterbalanced by the smaller size of the stomata, the hairiness and the thicker cuticle of the leaves; and also that, considering the stomata alone, the transpiration from the smaller but more numerous stomata of the upper leaves is not much greater than that of the lower leaves with the fewer but larger stomata. Darwin (1, pp. 436–437) considered that his experiments indicated that transpiration is regulated by stomatal aperture, because on the whole there was a parallelism in the curves of transpiration and of stomatal condition.

Hydathodes are not considered in relation to the stomata in any of the above papers. It was hoped that a comparison of the leaves of shoots of *Campanula rotundifolia* grown under different conditions would add something to our present knowledge of the distribution and other characters of the stomata and hydathodes.

STOMATA.

This investigation was begun to see whether the number or other characters of the stomata, such as their arrangement and size, vary on the lower and upper surfaces of the same leaf, or on the different leaves of the same plant, or on the leaves of different plants grown under varying conditions.

Results.

In the method finally adopted for determining the total area of the leaf, each leaf was placed directly on squared mm. paper, its outline was drawn and the number of squares within the outline was counted. After being cleared in eau de Javelle and stained slightly with Bismarck brown, the total number of stomata for each surface was counted and from the data obtained the average number of stomata per sq. mm. was estimated[1].

Basal, intermediate and upper linear leaves were examined[2] (see fig. 1), and it was found that the number of stomata per sq. mm. for the under surfaces of each leaf was almost equal, the upper surfaces on the other hand showed a rapid rise from the lower to the upper leaf.

	Under surface	Upper surface
Upper leaf	120	67
Middle leaf	120	54
Lower leaf	112	14

"*Whole*" *shoot*[3]. From the lowest leaf upwards the under surfaces showed a fluctuating rise. The upper surfaces of the leaves showed a marked rise, especially near the apex of the shoot. The average for both was highest for the upper leaves (see Table I, p. 62).

[1] The midrib was included in the estimation of the area of the leaf. The inclusion of the midrib, on which some stomata were always present, makes the number of stomata per sq. mm. slightly less than would otherwise be the case. The smaller veins did not affect the distribution of the stomata.

[2] From a shoot gathered on Benevenagh Mountain, Co. Derry.

[3] Grown in a garden, under normal conditions.

Normal shoot[1]. Both surfaces showed a rise and fall in the number of stomata and it was noted that the stomata on the upper surfaces were nearly four times more numerous on the top leaf than on the bottom one (see Table II, p. 62).

Shade shoot[2]. The under surfaces in this plant had a fairly uniform development of stomata from the base upwards. On the upper surfaces, however, the number varied to a greater extent (see Table III, p. 63). The number per sq. mm. was less on the whole than for the normal shoot (see Table II, p. 62).

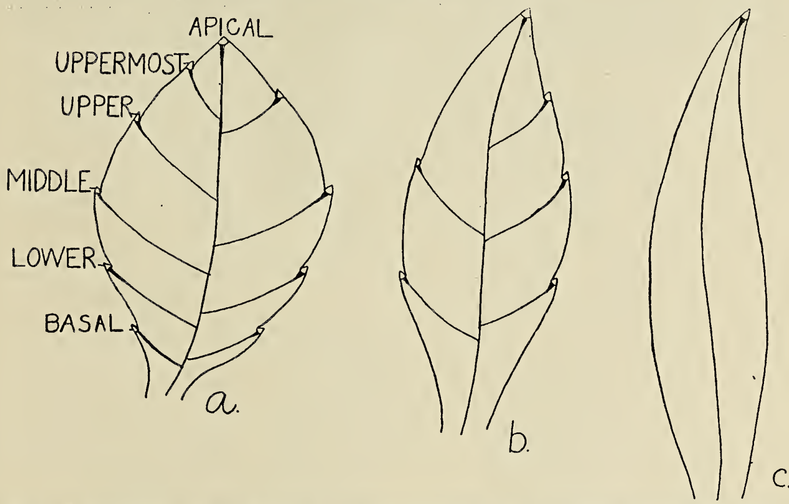

Fig. 1. Diagrams of (*a*) rotund, (*b*) intermediate, and (*c*) linear leaves, showing the position of the hydathodes.

Sun shoot[3]. This plant showed less fluctuation for the under surfaces, compared with the normal and shade shoots; with on the whole a higher number per sq. mm. On the upper surfaces of this plant for the first time, the numbers of stomata in some cases equalled or exceeded those obtained for the lower surfaces. The average number for both surfaces was much higher throughout the shoot than had been noted in the other plants examined (see Table IV, p. 63).

Arrangement of stomata. *"Whole" shoot.* The under surfaces of all the leaves had a row along the extreme margin, otherwise they were fairly evenly distributed. On the upper surfaces as a

[1] Grown in a garden, under normal conditions.

[2] Grown under a shady hedge, Newcastle, Co. Down.

[3] Grown on a dry, sandy heath, Edzell, Forfarshire.

rule there were no stomata seen till about the fourth or fifth cell inwards from the margin.

Normal shoot. On the under surfaces there was no regular marginal row till the sixth leaf from the base. In the leaves higher up this row was sometimes present; while on the twentieth leaf it was noted that there was a marginal row along one side of the leaf and not on the other. The stomata were arranged evenly on the upper surfaces of all the leaves.

Shade shoot. On the under surfaces generally speaking, the stomata were more numerous. The stomata were evenly distributed on the upper surfaces.

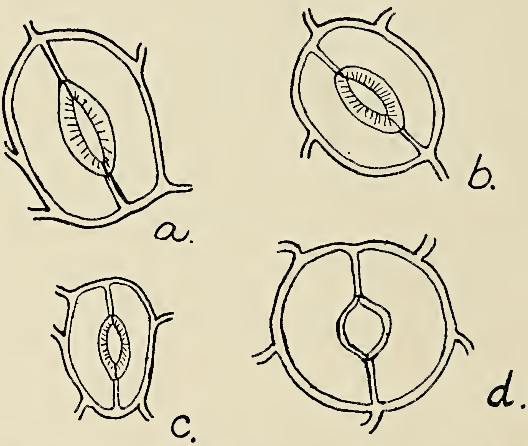

Fig. 2. (*a*) large, (*b*) medium, and (*c*) small stomata. (*d*) hydathode, from upper surface of a leaf. All × 500.

Sun shoot. On the under surfaces there was usually no marginal row present. The twenty-sixth leaf had an irregular marginal row and the top leaf had two more or less regular rows round the edge. Otherwise in that region the stomata were arranged irregularly. On the upper surfaces they were again evenly arranged.

Size of stomata. The under surfaces of the "Whole," Normal and Shade shoots, showed a varying number of large, medium and small stomata (see fig. 2) the shade shoot having more medium sized pores. The medium size predominated on the under surfaces in the sun plant and on the upper surfaces of all three types.

Seedlings. The cotyledonary leaves of the outdoor and indoor seedlings examined had about the same number of stomata per sq. mm. on their lower surfaces; but on the upper surfaces the average was considerably higher for the indoor seedling. The average, however, for both surfaces of the two seedlings was quite comparable with that noted for the lowest leaf of the normal plant. It was remarked that the stomata were all large and well developed.

		Lower surface		Upper surface	
Cotyledon	Area of leaf in sq. mm.	no. of stomata	av. no. per sq. mm.	no. of stomata	av. no. per sq. mm.
Outdoor seedling.					
2nd	6·1	443	72·62	16	2·62
1st	5·5	411	80·9	18	3·27
Indoor seedling.					
2nd	6·8	463	68·38	28	4·12
1st	6·4	517	80·8	41	6·5

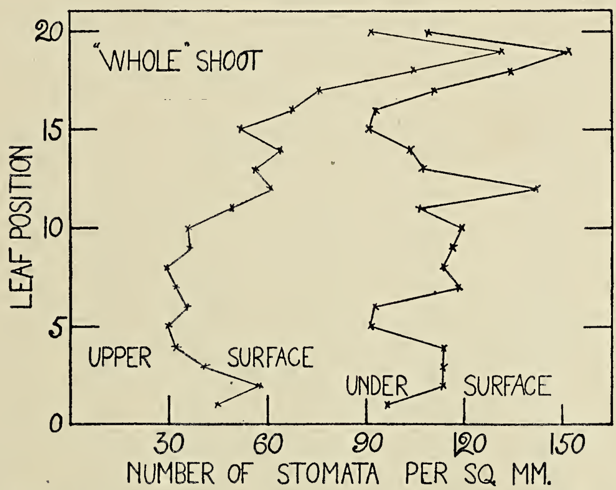

Fig. 3. Curves showing number of stomata per square mm. for upper and under surface of "whole" shoot according to position of leaf.

Curves were plotted, using the number of stomata per sq. mm. as abscissae and the position of the leaves, 1st, 2nd, etc., from the base upwards as the ordinates (see figs. 3–5).

Table I. Data concerning the stomata of the "Whole" Shoot.

	Leaf position on shoot 1st = lowest 20th = highest	Leaf area in sq. mm.	Lower surface		Upper surface		Av. no. of stomata per sq. mm. for both surfaces
			No. of stomata	Av. no. per sq. mm.	No. of stomata	Av. no. per sq. mm.	
Linear	20th	10·2	1,107	108·53	940	92·16	100·34
	19th	19·0	2,888	152·0	2,498	131·47	141·73
	18th	41·0	5,488	133·85	4,294	104·73	119·79
	17th	46·1	5,366	110·64	3,495	75·81	93·22
	16th	49·5	4,554	92·0	3,400	68·69	75·34
	15th	55·8	5,039	90·30	2,931	52·53	71·41
	14th	49·2	5,072	103·09	3,130	63·62	83·35
	13th	58·0	6,281	109·29	2,275	56·47	82·38
	12th	55·8	7,893	141·45	3,392	60·79	101·12
	11th	59·3	6,297	106·19	2,948	49·71	77·95
Intermediate	10th	68·3	8,129	119·2	2,461	36·03	77·52
	9th	68·0	7,865	115·66	2,479	36·45	76·05
	8th	68·0	7,724	113·59	2,016	29·65	71·62
	7th	65·2	7,778	119·29	2,050	31·44	75·36
	6th	43·4	4,015	92·51	1,429	32·92	62·71
	5th	33·0	3,005	91·06	987	29·91	60·63
	4th	29·6	3,359	113·48	962	32·50	77·99
Rotund	3rd	24·1	2,738	113·61	997	41·37	77·49
	2nd	14·7	1,666	113·33	848	57·69	85·51
	1st	13·0	1,250	96·15	579	44·54	70·34
		Total = 97,514			44,111		

Table II. Data concerning the stomata of the Normal Shoot.

Linear	24th	1·3	136	104·61	109	83·84	99·22
	23rd	4·4	300	62·12	235	53·41	57·76
	22nd	13·0	961	74·0	580	44·63	59·31
	21st	18·2	1,897	104·23	875	48·0	76·11
	20th	40·0	3,238	80·95	1,465	36·62	58·78
	19th	49·2	3,721	75·3	1,409	28·64	51·97
	18th	52·6	4,425	84·12	1,579	30·0	57·06
	17th	7·5	816	108·0	367	49·0	78·5
	16th	45·0	4,169	92·64	1,728	38·4	65·52
	15th	48·3	4,827	99·94	1,580	32·71	66·32
	14th	36·2	3,232	89·3	1,223	33·8	61·55
	13th	33·3	2,484	74·6	1,164	35·0	54·8
Intermediate	12th	38·3	2,496	65·17	1,284	33·53	49·35
	11th	34·2	2,348	68·65	1,264	37·0	52·82
	10th	38·2	3,308	86·6	1,923	50·34	68·47
	9th	40·2	3,800	94·53	2,028	50·45	72·49
	8th		8th leaf	was missing			
Rotund	7th	28·7	4,950	172·82	2,390	83·28	128·05
	6th	40·4	5,970	147·77	2,153	53·3	100·53
	5th	24·3	2,331	96·0	863	35·52	65·76
	4th	37·4	3,497	93·5	1,110	29·7	61·6
	3rd	47·7	3,410	71·49	1,207	25·3	48·35
	2nd	48·0	3,225	67·19	921	19·19	43·19
	1st	15·8	886	55·54	385	24·36	39·40
		Total = 66,427			23,842		

Table III. Data concerning the stomata of the Shade Shoot.

Leaf position on shoot 1st = lowest 15th = highest		Leaf area in sq. mm.	Lower surface		Upper surface		Av. no. of stomata per sq. mm. for both surfaces
			No. of stomata	Av. no. per sq. mm.	No. of stomata	Av. no. per sq. mm.	
Interm.	15th	31·2	3,600	115·38	947	30·35	72·86
	14th	42·44	5,000	117·92	1,926	24·2	71·06
	13th	37·0	4,467	120·72	1,243	33·6	77·16
	12th	41·4	3,920	94·68	1,129	27·27	60·47
Rotund	11th	42·5	4,132	97·22	827	19·46	58·34
	10th	28·2	2,409	85·42	682	24·18	54·80
	9th	26·8	2,144	80·0	569	21·23	50·61
	8th	16·6	1,456	87·7	474	28·55	58·12
	7th	13·1	900	68·7	443	33·81	51·25
	6th	10·4	1,010	97·11	558	53·65	75·38
	5th	12·0	744	62·0	448	48·17	50·18
	4th	17·9	1,906	112·12	989	58·18	85·15
	3rd	17·4	1,974	113·44	782	44·94	79·19
	2nd	13·8	1,660	121·0	333	24·13	72·56
	1st	23·8	2,400	100·0	574	24·12	62·06
		Total =	37,722		11,024		

The few upper leaves are not included in the table, as many of the stomata were immature (see fig. 1).

Table IV. Data concerning the stomata of the Sun Shoot.

Linear	40th	12·2	1,414	115·98	1,125	92·21	104·0
	39th	10·2	944	92·55	948	92·94	92·74
	38th	4·4	441	100·0	448	110·0	105·0
	37th	12·2	1,044	85·57	967	79·26	82·41
	36th	6·0	568	94·67	480	80·0	87·33
	35th	11·0	883	80·27	777	70·64	70·45
	34th	12·0	1,194	99·5	1,110	92·5	96·0
	33rd	11·0	1,045	95·0	802	72·91	83·95
	32nd	12·8	1,322	103·28	1,138	88·9	96·09
	31st	13·0	1,334	102·61	1,055	81·15	91·88
	30th	14·0	1,270	90·71	1,213	86·64	88·67
	29th	12·3	1,332	108·3	1,078	87·64	97·97
	28th	4·5	406	90·22	333	74·0	82·0
	27th	17·2	1,550	90·11	1,213	70·52	80·31
	26th	15·5	1,822	111·1	1,205	77·74	94·42
	25th	24·3	2,509	103·25	1,626	66·91	85·08
	24th	25·2	2,660	105·55	1,404	55·71	80·63
	23rd	29·0	2,310	79·65	1,646	56·74	68·19
	22nd	16·6	1,279	77·05	911	54·88	65·96
	21st	21·4	2,003	93·6	1,669	78·0	85·8
	20th	19·2	2,153	112·24	1,553	79·84	96·04
	19th	22·4	2,059	91·92	1,680	75·0	83·46
Interm.	18th	33·3	2,912	86·46	2,087	62·67	74·56
	17th	25·6	2,823	110·27	1,895	74·02	92·14
	16th	26·0	2,407	92·58	1,811	69·65	81·11
	15th	18·0	2,050	113·89	1,320	73·33	93·61
		Total =	41,734		31,514		

The fourteen lower leaves had fallen off (see fig. 1).

Conclusions.

The average number of stomata per sq. mm. on the upper surfaces shows a steady rise from normal to sunny conditions (see Tables II to IV, pp. 62 and 63). This is not the case for the under surfaces, a probable reason being that the lower surfaces of leaves are always more or less in shade independent of habitat. The stomatal curves (see figs. 3–5) for the normal and shade shoots overlap: this is possibly due to the fact that the lower leaves of the normal shoot were shaded by other shoots.

The difference in the total number of stomata for the under and upper surfaces respectively of the "whole," normal, shade and sun shoots is instructive (see Tables I, II, III and IV, pp. 62 and 63). The normal shoot has about three times as many stomata on the under surfaces as on the upper; the shade shoot has more than three times the number on the under surface as compared with the upper, while for the sun plant the numbers approximate much more nearly for both surfaces. The "whole" shoot was grown under normal conditions, but the early summer of 1917 was drier and warmer than that of 1920 and this would account for the higher average number of stomata per sq. mm. compared with the number for the normal shoot examined in 1920 (see Tables I and II, p. 62).

The average number of stomata per sq. mm. for the under and upper surfaces of all the leaves of the shoots taken together was as follows:

	Under surface	Upper surface
Sun shoot	97·21	73·4
"Whole" shoot ...	111·93	50·63
Normal ,, ...	89·5	32·12
Shade ,, ...	100·96	29·5

It is evident that numerically the sun plant has more stomata per unit area than the other shoots, especially on the upper surface; and suggestions are put forward later to account for this fact.

Professor Yapp's work showed that the stomata increased in number on the higher leaves of *Spiraea Ulmaria* and did so more markedly on the plant growing in a sunny situation. Although the stomata occurred only on the under sides of the leaves, those data have more bearing on *Campanula rotundifolia* than any of the other work cited. Contrary to Tschirch's results, *Campanula rotundifolia* has more stomata per unit area in the sunny exposed situation than in the normal or shade conditions. This latter point is clearly shown

by the curves (see figs. 4 and 5, p. 67). Therefore it is concluded that the position of the leaf on the shoot and the habitat may be factors in the number of stomata present. Also, considering the number of stomata alone, it looks as if there was more transpiration from the sun shoot than from either the normal or shade shoots.

Other factors, however, may serve to lessen the effect of the more numerous stomata of the sun shoot. Foremost is the size of the stomata and especially of their pores. The large stomata on the under surfaces of the lower leaves of the normal and shade plants were absent from the under surfaces of the sun shoot. In most instances where there was an exceptionally large number of stomata per sq. mm. it was noticed that the stomata were small and had small pores (cp. 7, pp. 827–828). Therefore the transpiration might be little more from those leaves with a large number of small stomata, than from those where the stomata were larger but fewer. It may seem peculiar that the sun plant should form so many stomata, since considering transpiration alone, it might be inferred that the plant would suffer by losing more water than it could well spare in such a situation. Possibly, however, the question of photosynthesis is of such importance that the plant responds specially to it owing to the favourable conditions, and counterbalances the stomatal increase by making use of other devices to lessen water-loss which will be mentioned later. Haberlandt (3, p. 473) suggests in this connection that under these circumstances a current of air travelling through the whole thickness of the leaf is useful from the point of view of gaseous exchange.

The arrangement of the stomata was the same in all the shoots for the upper surfaces of the leaves, therefore neither leaf position nor habitat appears to be important. The arrangement was variable near the margin for the under surfaces of the leaves, and it is suggested that this is due to leaf position and possibly to other factors. It was concluded that the isobilateral tendency of the upper leaves of the normal shoot, and especially those of the sun plant, might be a factor in the equalization of the stomata on both surfaces of these leaves. Further, the linear shape of the upper leaves and also their thicker cuticle, as well as the smaller size of the cells in the upper leaves, would tend to reduce transpiration.

Miss Tenopyr (4, p. 216) states that "in *Campanula rotundifolia* the broad radical leaves had epidermal cells of an average length of ·04 mm. and breadth of ·039 mm. Those of linear cauline leaves had cells ·034 × ·032 mm., and transitional leaves ·038 × ·034 mm.

This agreed with Sierp's similar observations in *Mirabilis jalapa, Nigella damascena* and *Pisum sativum*. The higher the leaf the smaller its cells." The results obtained in 1917 when examining the leaves of the Benevenagh plant were thus confirmed. These factors would probably counterbalance the effect of any stomatal increase on the upper leaves of the shoots. Conversely the shade plant had more rotund and thinner leaves than the normal shoot. The part that hydathodes play in connection with water-loss in the leaves of *Campanula rotundifolia* examined, will be considered in the next section.

HYDATHODES.

While the leaves of the various plants were being examined for stomatal distribution, it was thought that the number of hydathodes which occurred on their upper surfaces might show some relation to their position on the leaf, to the position of the leaf on the shoot and to the environment of the plant.

The position and number of the hydathode groups on each margin of the upper surfaces were noted as shown in fig. 1. The total number of pores per leaf was ascertained and the results are given in the Tables V to VII, pp. 68 and 69) and are shown in the graph (see fig. 6, p. 67).

The hydathodes were developed on the lower leaves on slight marginal projections at the club-shaped terminations of the principal veins and the midrib. Usually there were three groups of hydathode pores on each margin, occasionally there were four or even five, nearly opposite each other, besides the apical one (see fig. 1).

The number of pores in each group varied, being most numerous in the apical group with one or two exceptions; and decreasing from apex to base of each leaf. The total number of pores per leaf shows a decrease from base to apex of each shoot. In a few instances the basal hydathodic organs had only one or two pores. The intermediate type of leaf had fewer marginal groups and only an apical one was present on the upper linear leaves. The individual pores were observed to be larger and clearer on the shade plant than on the normal or the sun shoot. The three leaves had the following number of pores present; on the lower leaf 32 pores; on the middle leaf 20 pores; and on the upper leaf 7 pores.

On the "whole" shoot the marginal groups were irregular in distribution, two being the highest number observed on either

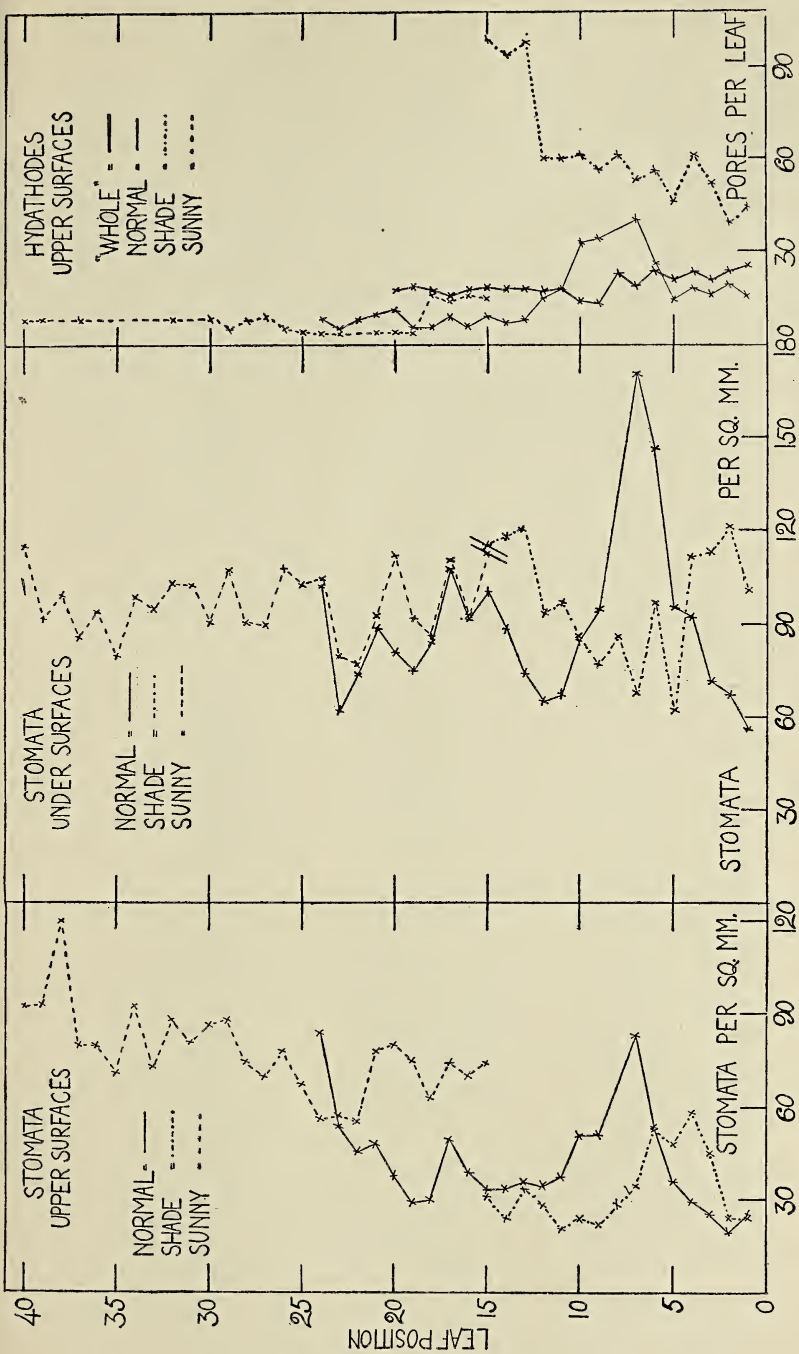

Fig. 4. Stomata per sq. mm. on upper surfaces according to position of leaf.

Fig. 5. Stomata per sq. mm. on under surfaces according to position of leaf.

Fig. 6. Hydathode pores per sq. mm. on upper surfaces according to position of leaf.

Table V. Data concerning the hydathodes of the "Whole" Shoot.

	Leaf position on shoot 1st = lowest 20th = highest	Apical group	Groups right margin	No. of pores right margin	Groups left margin	No. of pores left margin	Total no. of pores per leaf
Intermediate Lin.	20th to 9th	13 to 19	—	—	—	—	13 to 19
	8th	18	—	—	1	middle = 5	23
	7th	13	—	—	1	middle = 3	16
	6th	15	2	middle = 4 lower = 2	1	middle = 3	24
	5th	12?	1	middle = 4	2	middle = 3 lower = 2	21?
	4th	11	2	middle = 4 lower = 2	2	middle = 4 lower = 2	23
Rotund	3rd	14	1	middle = 2	1	middle = 4	20
	2nd	13	2	middle = 3 lower = 2	2	middle = 3 lower = 2	23
	1st	14	2	middle = 2	2	middle = 4	25
						Total =	381

Table VI. Data concerning the hydathodes of the Normal Shoot.

	Leaf position on shoot	Apical group	Groups right margin	No. of pores right margin	Groups left margin	No. of pores left margin	Total no. of pores per leaf
Intermediate Lin.	24th to 13th	5 to 11	—	—	—	—	5 to 11
	12th	13	—	—	1	middle = 2	15
	11th	9	2	upper = 4 middle = 3	2	upper = 1 middle = 1	18
	10th	10	3	upper = 5 middle = 2 lower = 3	3	upper = 3 middle = 5 lower = 5	35
	9th	8	3	upper = 6 middle = 4 lower = 4	3	upper = 6 middle = 4 lower = 2	34
	8th	This leaf	was mi	ssing			
Rotund	7th	10	3	upper = 5 middle = 6 lower = 3	3	upper = 6 middle = 6 lower = 4	40
	6th	6	3	upper = 4 middle = 5 lower = 3	3	upper = 2 middle = 2 lower = 4	26
	5th	5?	2	upper = 1 middle = 2	2	upper = 4 middle = 2	14
	4th	4?	2	middle = 3 lower = 3	2	middle = 5 lower = 2	18
	3rd	4	2	upper = ? lower = 3	3	upper = ? middle = 3 lower = 1	16
	2nd	4	2	— middle = 4 lower = 2	3	upper = 4 middle = 4 lower = 1	19
	1st	5?	2	upper = 4 middle = 4	1	middle = 3	15
						Total =	345

The ? indicates that the number is correct to within one or two pores.

Table VII. Data concerning the hydathodes of the Shade Shoot.

	Leaf position on shoot 1st = lowest 15th = highest	Apical group	Groups right margin	No. of pores right margin	Groups left margin	No. of pores left margin	Total no. of pores per leaf
Intermediate	15th	20	4	upper = 15 middle = 9 lower = 6 basal = 5	5	uppermost = 8 upper = 13 middle = 11 lower = 6 basal = 6	99
Intermediate	14th	22	4	upper = 15 middle = 11 lower = 8 basal = 4	4	upper = 12 middle = 9 lower = 8 basal = 5	94
Intermediate	13th	21	4	upper = 15 middle = 10 lower = 9 basal = 5	4	upper = 13 middle = 7 lower = 12 basal = 6	98
Intermediate	12th	17	3	upper = 11 middle = 12 lower = 7	4	upper = 10 middle = 9 lower = 8 basal = 1	75
Rotund	11th	11	3	upper = 15 middle = 8 lower = 9	4	upper = 12 middle = 10 lower = 8 basal = 2	75
Rotund	10th	13	4	upper = 14 middle = 11 lower = 9 basal = 3	3	upper = 11 middle = 9 lower = 6	76
Rotund	9th	12	3	upper = 8 middle = 10 lower = 6	3	upper = 3 middle = 8 lower = 9	56
Rotund	8th	15	3	upper = 7 middle = 8 lower = 7	3	upper = 9 middle = 7 lower = 8	61
Rotund	7th	12	3	upper = 9 middle = 6 lower = 4	3	upper = 9 middle = 8 lower = 5	53
Rotund	6th	15	3	upper = 10 middle = 8 lower = 4	3	upper = 7 middle = 7 lower = 5	56
Rotund	5th	14	3	upper = 8? middle = 7? lower = 3?	3	upper = 7 middle = 5 lower = 4	46
Rotund	4th	14	3	upper = 9 middle = 8 lower = 6	3	upper = 10 middle = 8 lower = 6	61
Rotund	3rd	12	3	upper = 10 middle = 10 lower = 4	3	upper = 6 middle = 7 lower = 3	52
Rotund	2nd	8	3	upper = 9 middle = 5 lower = 3	2	upper = 9 middle = 5	39
Rotund	1st	9	2	— middle = 9 lower = 9	2	middle = 9 lower = 8	44
						Total = 985	

The ? indicates that the number is correct to one or two pores (see fig. 1)
For data concerning the hydathodes of the Sun Shoot, see p. 70.

margin of the leaf; and marginal groups ceased altogether after the eighth leaf from the base. The apical hydathodic organs were large, especially towards the top.

The lowest leaf of the normal shoot had 15 pores and the number gradually increased till the seventh, which had a maximum of 40; then a fall occurred, at first gradual, but very marked in the case of the eleventh leaf where the number was 18, whereas the tenth had 33. From the thirteenth leaf to the top or twenty-fourth one, only an apical group was present, with a varying number of pores.

The shade plant showed a strong contrast to the normal one. Both the rotund and intermediate leaves had more marginal groups of hydathodes and the individual pores were larger. The lowest leaf had 44 pores and with a few exceptions these increased in number till on the fifteenth 99 were counted.

In the sun shoot the scars of the first fourteen leaves alone remained. From the fifteenth to the eighteenth leaf there was an apical group of 8 pores, and in addition the right margins had 1–2 groups, comprising 3–8 pores. From the nineteenth to the fortieth leaf only an apical group of 4–9 pores was present. The reduction in the number of pores in the sun plant is very noticeable compared with the number in the normal plant, and this difference is much more marked between the sun plant and the shade plant.

Total number of pores in the several shoots:

"Whole" = 381, Normal = 345, Shade = 985, Sun = 153

The cotyledonary leaves of the outdoor seedling had each an apical group of 4 pores, the corresponding leaves of the shade plant having each 5 at the apex.

CONCLUSIONS.

1. The position on the leaf.

The hydathodes invariably occur over the marginal terminations of veins, particularly the midrib. It may be concluded therefore that they occupy a definite position on the leaf in relation to the conducting system.

2. The position of the leaf on the shoot.

Three or occasionally four hydathode groups were developed on each margin of the basal leaves; they were fewer in number on leaves of intermediate type, and the upper linear leaves possessed only the apical group. Epidermal transpiration from the upper

linear leaves is probably reduced to a minimum as the cuticle is slightly thicker than in the intermediate or basal leaves. It is generally recognised that of two leaves of the same volume, if one is flat and thin it will lose more by evaporation than a narrow thicker one.

Thus towards the apex of the shoot the leaves show an approach to xeromorphy which includes the degree of development of the hydathodic organs. The number of hydathodes present bears a distinct relation to the position of the leaf on the shoot. The above conclusions were applicable in varying degrees to the three leaves, to the "whole" shoot and to the normal, sun and shade shoots. The cotyledonary leaves appear to be exceptional, as although they were basal in position, a single apical hydathode group was present.

3. The environment.

From the fact that the hydathodes on the shade plant had more numerous and larger pores for comparable leaves than either the normal or sun shoots, it would seem that environment is an important factor in the development of these water-secreting organs. As they were most numerous at the base of the shoots, these pores are probably very efficient in getting rid of superfluous water. The danger of the internal tissues being flooded, in the absence of accessory means of increasing the water-loss, would be most acute in the shade and normal plants. The lower leaves were not present in the sun shoot, but the above suggestion would hold good, although the difference between that shoot and the normal one is not so marked. In such, a danger of internal flooding in the leaf would not be so acute, and further, the presence of a larger number of stomata on the upper surfaces of the leaves of the sun plant is probably correlated with this decrease in water-secreting pores.

SUMMARY.

Stomata.

1. The number of stomata per sq. mm. varies in *Campanula rotundifolia*, increasing especially on the upper surface with a higher position of the leaf on the shoot; and on the under surface also with increase of illumination and dryness of the habitat of the plant.

2. The increase in number of stomata per sq. mm. in the sun shoot as compared with the normal shoot is suggested to be due to increased photosynthesis, as involving the utilisation of more

carbon dioxide; the water-loss at the same time being reduced by reduction in the number of hydathodes, and by the more nearly erect position of the leaf.

3. The arrangement of the stomata varied according to the leaf surface, there being sometimes a marginal row on the under surface which was wanting on the upper side; but this character is variable.

4. The stomata on the under surfaces varied markedly in size for the lower leaves of the normal and shade shoots, being large, medium or small; while on the upper surfaces in these shoots and on both sides of the leaves of the sun plant the medium size occurred.

Hydathodes.

1. Hydathode groups were present on the upper surfaces of all the leaves examined.

2. They were most numerous towards the bases of the shoots, and only an apical group was present on the upper linear leaves.

3. From the data obtained it is concluded that hydathodes are developed to a degree which is dependent upon the development of the vascular system of the individual leaves, upon the position of the leaves on the shoot, and also upon the habitat of the plant.

Acknowledgments are due to Professor R. H. Yapp, at whose suggestion the work was commenced, for material; to Mr B. M. Griffiths for advice; also to Professor J. Small for material and his assistance in the preparation of the paper for publication.

REFERENCES.

(1) DARWIN, F. On the relation between Transpiration and Stomatal Aperture. *Phil. Trans. Roy. Soc., London*, B, **207**, pp. 436–437. 1916.

(2) DELF, E. M. Transpiration and Behaviour of Stomata in Halophytes. *Ann. Bot.*, **25**, pp. 500–501. 1911.

(3) HABERLANDT, G. *Physiological Plant Anatomy.* Engl. transl. 1914.

(4) TENOPYR, L. A. On the size and shape of cells in leaves of different forms on the same plant (*Campanula rotundifolia* and *Lobelia Erinus*). *Bull. Torrey Bot. Club*, Feb. 1918; *ex Science Progress*, No. 50, Oct. 1918, p. 216.

(5) TSCHIRCH, A. Ueber einige Beziehungen des anatomischen Baus der Assimilationsorgane zu Klima und Standort, mit specieller Berücksichtigung des Spaltöffnungs-apparates. *Linnaea*, N.F. **9**, p. 173. 1880–1882.

(6) WEISS, A. Untersuchungen über die Zahlen- und Grössenverhältnisse der Spaltöffnungen. *Jahrb. f. wiss. Bot.*, **4**, pp. 166–167. 1865.

(7) YAPP, R. H. *Spiraea Ulmaria* L., and its bearing on the problem of xeromorphy in marsh plants. *Ann. Bot.*, **26**, pp. 826–828. 1912.

THE HYDRION DIFFERENTIATION THEORY OF GEOTROPISM: A REPLY TO SOME CRITICISMS

By JAMES SMALL

Having read with interest a recent criticism[1] of the "creaming" part of the hydrion differentiation theory of geotropism, the writer feels indebted to Professor V. H. Blackman for affording him an opportunity of making clear certain points in the theory which seem obscure to several correspondents. The publication of this theory was really an honest attempt to provide a working hypothesis for the elucidation of the nature of geotropic response. The theory is therefore open to considerable amendment and even to complete rejection, if and when experimental data or other known facts which are of sufficient weight are brought forward. But so far as purely theoretical considerations are concerned there is certainly no need to stumble over a particle as large as 0·0002 mm. in radius.

Throughout his article Professor Blackman reasons from the *assumption* that "the protoplasmic [particles] in question are ultra-microscopic" (*op. cit.* p. 40). He even writes (*loc. cit.*): "As by the author's hypothesis the particles are ultra-microscopic," and as this idea seems to be shared by a few others, the writer apologises for any ambiguity which may have given rise to this misunderstanding. So far as he is aware the term "ultra-microscopic" does not occur in any of the papers previously published. The hypothesis as originally stated[2] is that: "The protoplasm was conceived to be an *emulsion* of protein or protein-lipoid particles in a colloidal protein medium."

Reference was also made to the Brownian movement of these particles and to the *suspensoid* structure of the plasma membrane. In an abstract[3] reference was again made to the *emulsion structure*. The term "emulsion" rather than "colloidal solution" has been used always, as far as the writer is aware, because of the

[1] *New Phytologist*, **20**, No. 1, p. 38. 1921.

[2] *New Phytologist*, **19**, Nos. 3 and 4, p. 50, § 3. 1920.

[3] *Linnean Society*, 18th March, 1920.

comparatively large size of the particles which are considered to act in the "creaming" process.

At the same time, even in colloidal solutions *microscopic* particles can be distinguished in some cases. Linder and Picton[1], for example, "recognised four kinds of sols: *α, visible in the microscope*." Further Taylor (*op. cit.* p. 11) states that: "The upper limit [of colloidal heterogeneity] has been fairly definitely established, and lies *above the limit of microscopic visibility*." He gives 10 μ as this upper limit; "particles between these limits (10 μ and 0·1 μ) are termed *microns* in Zsigmondy's nomenclature." According to a recent report[2] on Ultramicroscopy "the lower limit for the *micron* is conventionally fixed at ·2 μ and corresponds with the limit of microscopic visibility as determined by Johnston Stoney." However, in order to remove any further ambiguity, the size of the particles which are supposed to cream has been given definitely[3] as "very small, almost ultramicroscopic[4] (i.e. ·2 μ to ·8 μ radius), or quite ultramicroscopic (i.e. less than ·1 μ radius)." Brownian movement is shown by such particles, "at this stage [0·1 μ] the phenomenon known as the Brownian movement, just observable at about 10^{-3} cm. [= 10 μ], is well developed[5]."

Keeping in mind that the "creaming" particles may be anything up to 0·8 μ in radius, we may be allowed to readjust the data given in the first section of Professor Blackman's article. As pointed out in that paper, Perrin found "that for gamboge particles of radius 0·21 μ the concentration was halved for each rise in height of 30 μ." Since a meristem-cell in a root-tip averages 20 μ to 40 μ in diameter, this degree of difference in concentration would seem to satisfy the requirements of the "creaming" hypothesis.

One other point may be noted from § 1. It is stated that: "As is well known, there is no obvious settling of colloidal solutions." Taylor (*op. cit.* pp. 56–57) gives amongst "the methods which connect the size of the particle with other properties of the sol," "(3) the *velocity of sedimentation*," and he also gives the Stokes' Law equation as the basis of this method. It is true he adds that: "It

[1] See *The Chemistry of Colloids*, by W. W. Taylor, p. 58. London. 1920.

[2] B.A. Rep., Cardiff, 1920. Third Report of the Committee on Colloid Chemistry, p. 32.

[3] See *A Textbook of Botany*, J. Small, p. 347. Churchill. London. 1921.

[4] Since Abbe placed the lower limit of microscopic visibility at 0·8 μ to 0·2 μ this phraseology is quite justified (see *An Introduction to the Physics and Chemistry of Colloids*, by E. Hatschek, p. 24. London. 1919).

[5] Taylor, *op. cit.* p. 11.

is only applicable when the dispersity is low, for if $r = 10\ \mu\mu$ [0·01 μ] the time to fall 0·1 mm. [100 μ] is 7 hours." In the above-mentioned report we also find under Stokes' Law that, using this equation, "we have a ready means of determining accurately their size from diameters of 1 mm. to and *beyond the microscopic limit*," and again (*op. cit.* p. 36) that this "method cannot conveniently be used for *submicrons* of *less than* 20 $\mu\mu$ [0·02 μ] diameter." Also (*loc. cit*) certain ultra-microscopes "when arranged horizontally are well suited for the purpose of determining the radius of *submicrons* from *their speed of settlement by the application of Stokes' Law*." From these quotations it would appear that "settling" in colloidal solutions is not only well known, but is carefully measured by some of those who deal in a practical way with such material.

In the second section of his article Professor Blackman raises several points which are best considered *seriatim*. (1) The *time factor*, with particles of radius 0·2 μ to 0·8 μ, does not present serious difficulties (see below for calculations). (2) "Perrin...allowed three hours for the completion of the process." This statement is brought forward to support the view that particles even of 0·2 μ radius would cream too slowly, but Professor Blackman on a later page emphasises the fact that stimulation continues for some time after its commencement. Now it is the *beginning* of stimulation which occurs soon after the organ is displaced, and therefore we should consider, not the time taken by the particles to reach a stable equilibrium (as they did in three hours with Perrin's gamboge), but rather the time which elapses before the redistribution of the particles becomes apparent. This time is indicated by Perrin, who states[1] that when the *uniform emulsion* is placed in a cell 100 μ high "a *few minutes* suffice for the lower layers to become *manifestly* richer in granules than the upper layers." The resulting stimulation, if any, would, therefore, *begin in a few minutes and continue for about three hours*, thus satisfying the requirements both of rapid and of continued excitation (see also below). (3) Perrin's data with a medium of viscosity 125 times that of water are next quoted. From this one infers that the critic considers protoplasm to be of a similar viscosity, but on the following page he takes a viscosity twice that of water for the protoplasmic medium. This is a wide range, and more restricted estimates are fortunately available.

[1] *Brownian Movement and Molecular Reality*, by J. Perrin. Eng. trans. p. 41. London. 1910.

Ewart[1] states that "we have weighty reasons for considering the viscosity of the main bulk of the streaming protoplasm to be within the limits ·04 to ·2 at 18° C." Since Siefriz[2] has shown that the active protoplasm of young cells has a minimum viscosity (i.e. something *below* ·037), it is quite reasonable to take Ewart's lower limit (·04) as the viscosity of the protoplasm in the meristem. (4) Professor Blackman next states that my conclusion that the "creaming" is governed by Stokes' Law is certainly mistaken. As pointed out above (p. 72) the application of Stokes' Law is commonly regarded as an accurate method of measuring the rate of fall of particles (even down to ·02 μ diameter) which are heavier than the medium, and there is no reason to suppose that a density difference in the opposite sense renders futile the application of a general law like that of Stokes. Although the ultimate distribution of even very heavy particles is determined by the exponential "rarefaction law," the initial stages of fall must be governed by Stokes' Law. Perrin makes this point clear, when he states (*op. cit.* p. 35) that: "It is necessary to employ a *capillary* tube to *avoid the convective movements*" which occur in *wider* tubes; that in "a shallow cylindrical vessel about 100 μ in height" (*op. cit.* p. 31), "if our kinetic theory is exact, this [uniform] distribution will change from the time the preparation is left at rest" (*op. cit.* p. 41); and that this change is obvious in a few minutes (see above). Perrin is even more explicit in the extrapolation from Stokes' Law which he gives, adding (*op. cit.* p. 40) that: "The preceding experiments show that this law is valid in the domain of microscopic quantities, and the verification pushed even to the threshold of ultramicroscopic magnitudes, scarcely leaves a doubt that the law may still be valid for the far smaller granules of ordinary colloids, or for the *large ions* found in gases." And further (*op. cit.* p. 76), "Now the reasoning of Einstein supposes the *law of Stokes* to be valid. It is therefore probable that this law, the exactitude of which I have proved directly as far as dimensions of the order of a tenth of a micron (No. 21), still remains exactly verified for large molecules, the diameter of which *does not reach the thousandth of a micron*. It will permit us presently to apply the law of Stokes with safety to the case of ions in movement through a gas."

Stokes found that his law is valid so long as the radius of the

[1] *On the Physics and Physiology of Protoplasmic Streaming in Plants*, by A. J. Ewart, p. 19. Oxford. 1903.

[2] *Botanical Gazette*, **70**, p. 360, Nov. 1920.

particle is small compared with the *critical radius*, which is $\frac{\eta}{v\rho}$, where η = viscosity of medium, ρ = density of medium, and v = velocity of particle[1]. Arnold found that the law was valid so long as the radius of the particle was less than ·6 of the critical radius (*op. cit.* p. 96); while Millikan working with gases found that Stokes' Law becomes invalid only when the radius of the sphere is comparable to "the mean free path" of a gas molecule, and mentions (*op. cit.* p. 98) that the "holes" in the medium or the mean free paths are negligibly small "when the drop falls through a liquid."

It seems clear, therefore, that although the exponential "rarefaction law" governs the final state of equilibrium, Stokes' Law must govern the actual falling or "creaming" of the particles. We may have to apply a correction, as Perrin (*op. cit.* p. 34) points out, for the recoil of the particles as they accumulate at the bottom or the top of the cell, i.e. as they approach their exponential distribution, but this would be a correction for an aberration from the basal law (Stokes') governing all slow movements of spheres through a relatively viscous medium under a constant unidirectional force. Further, although the smaller "ultra-microscopic granules within the narrow confines of a cell only 0·05 mm. in height must always be little removed from their limiting distribution," the larger microscopic or almost ultramicroscopic particles in the cell will be far removed from their limiting distribution, even in a cell only 30 μ in height, and they will *begin* to become redistributed in a few minutes as observed for Perrin's gamboge particles.

As an example of how far such particles may be removed from their stable distribution it will be sufficient to point out that Perrin (*op. cit.* p. 43), with particles of about 0·3 μ radius, found a height of 30 μ sufficient to lower the concentration of the granules *to* one tenth of its value. In this case 10 μ, not "30 *millimetres*," in the cell were equivalent to 6 kilometres in the air.

As an example of what is supposed to occur, we will take milk, regarded as an ideal emulsion and containing fats as a disperse phase with a protein solution as the continuous phase. The density difference in an average good sample of milk is 0·17, which is smaller than the density difference in Perrin's experiments, as Professor Blackman suggests it would be in the cell. Viscosity we may

[1] See *The Electron*, by R. A. Millikan, p. 95. Chicago. 1917. With particles moving 1·55 μ in 7 minutes in a medium of density 1·03 as calculated below the critical radius is about one kilometre.

legitimately take as being ·04 (see above, p. 76). Then applying Stokes' Law, we find the rate of creaming to be 1·55 μ in the 7 minutes of Presentation Time[1] with particles of ·2 μ radius, and 24·8 μ in the same time with particles of ·8 μ radius. Since the particles *begin* to cream almost immediately, when the organ is laid horizontally, a very short Perception Time can be detected by suitably delicate apparatus[2].

An interesting point is that, with short periods of intermittent stimulation on a klinostat, each particle would remain for some time during rotation very nearly[3] at the point which it had reached during each successive stimulation; and no curvature would take place until the total potential difference produced by the "creaming" particles was sufficiently strong to develop in its turn a turgor difference (between upper and lower sides of the organ) which would be sufficient to overcome the mechanical rigidity of the organ. In this way we arrive at some sort of explanation of the occurrence of Presentation Time and Relaxation Time[4]. Therefore, whereas it may "seem impossible to correlate active electrical and mechanical reaction occurring in a few seconds or minutes with a redistribution of plasma particles requiring days for its accomplishment," when we assume that at least some of the particles are near but not under the limits of microscopic visibility, we can carry the correlation of the redistribution of such particles with geotropism into practically all the details of that most obscure physiological phenomenon.

In the third section of his article Professor Blackman raises another difficulty, namely the disappearance of potential differences when the "creaming" is completed. It is quite reasonable to suppose that protoplasm, like most colloidal solutions and emulsions, contains dispersed particles which vary considerably in size. The larger *microns* are supposed to bring about the rapid perception and the initial action current by their relatively quick "creaming." But Professor Blackman so ably expounds in the earlier sections of his paper the slow rate of creaming of the *smaller* particles, that it is scarcely necessary to point out that these *submicrons*, too, may be taken as electrically charged; and that by their *slow* creaming,

[1] For the broad-bean root. [2] See *Proc. Roy. Soc.* B. **90**, p. 351. 1918.

[3] The "outward" movement according to Gibbs' Law being slower than the "creaming."

[4] Would heavy particles which stick and then produce "a sudden precipitation of geo-electric response" show any definite Relaxation Time?

"requiring days for its accomplishment," these particles may *slowly* produce potential differences which would continue the action current[1] *initiated* by the "creaming" of the larger particles. Now, if we suppose a potential difference to be developed in each cell on displacement of the organ, we have the possibility of an action current for several days. Further, *only meristems are supposed to be geotropically perceptive*, at any rate in the higher plants. Cell division in meristems is frequent, and some cells are always in the process of division. During cell division there is naturally a more or less complete redistribution of the dispersed particles, and each daughter cell may be considered as showing "creaming" for at least several days after its formation. It will be remembered that, when the main apical meristem becomes inactive in any way, its functions are taken over by a lateral branch. Since the "normal polarity current" is dependent upon the meristematic activity and controls the angle of the lateral organs, the disappearance of that activity involves the disappearance of the control of the lateral organs, until one of these assumes the vertical position, and takes over control by producing a "normal polarity current" instead of an "action current."

Professor Blackman then proceeds to quote two experiments by Bose. These can be dealt with briefly. In the first there is no evidence that the electrode position in the endodermis was distinguished from a close approximation to the adjacent meristematic region of the cambium, which might have been the gravity-perceptive region in that case. The second is surely a special case, since Bose himself has recently[2] stated that "the electrical response is found to increase as the sine of the angle of inclination," and he is supported *on this point* by the observations of Fitting and the writer[3]. Since the phenomenon is exceptional, even in Bose's experiments, it follows that a special enquiry is necessary and a special explanation probable.

Professor Blackman supposes that my theory "rejects the movement of comparatively large cell particles (such as starch grains) as the first step" and quotes the experiments by Bose in support of the statolith hypothesis. The presence of statoliths and of gravity

[1] Possibly to a lesser degree, but the smaller movement might be compensated by the greater number of smaller particles and the resulting possible increase in total potential difference.

[2] *Nature*, 22nd July, **105**, p. 650.

[3] See *Proc. Roy. Soc.* B. **90**, pp. 349–360. 1918.

perception have not yet been connected logically as cause and effect; they are as yet only frequently concomitant circumstances. The presence of "creaming" bodies on the other hand can be connected causally with the series of changes which are supposed to result in geotropic curvature, and the granular appearance of cytoplasm is too well known to require any special demonstration of the presence of bodies which may "cream." Let any reader carefully compare the numbers of phenomena which find an explanation under the statolith hypothesis with those which find at least a possible and reasonable basis in the chemistry and physics of the cell under the hydrion differentiation theory, and then say which theory is the more scientific. The nature of the geotropic response, if the statolith theory be accepted, is one of the most obscure of physiological phenomena.

On the other hand, the hydrion differentiation of the expressed sap is an experimentally demonstrated *fact* in the case of many roots and many stem structures[1]. Roots are well known to be acidic, beyond a P_H 4·5, and the single fact that chlorophyll is stable only in a relatively alkaline medium[2] makes the relative alkalinity of green stem structures an obvious fact, since there is not a more widespread indicator. It may be objected that the "reaction" of the cytoplasm has not been investigated, but there is no reason for supposing that it is differentiated in the *opposite* sense[3].

If the propagation of the gravity stimulus is due to potential differences giving an electric current which modifies the permeability of the cells[4], the direction of that current and of subsequent curvature is almost certainly determined by the movement of electrically

[1] See A. R. Haas in *Jour. Biol. Chem.* **27**, p. 225, 1916; J. Hempel in *Compt. Rend. d. trav. d. Lab. d. Carlsberg*, **13**, Liv. I, 1917; and H. Kappen in *Landw. Versuchst.* **91**, p. 1, 1918 (Abst. in *Bot. Abst.* II, 4, p. 143. 1918).

[2] Cf. *Practical Plant Biochemistry*, by M. W. Onslow, pp. 37–38. Cambridge. 1920.

[3] Cf. A. R. Haas in *Bot. Gaz.* **63**, p. 232. 1917.

[4] That it is permeability which acts in producing the turgor differences seems to be the only alternative left since the viscosity differences recorded by Weber (*Oesterr. Bot. Zeitschr.* **64**, p. 439. 1914, also *Jahrb. f. wiss. Bot.* **57**. 1917) have been shown by Zollikofer (*Ber. D. Bot. Gesell.* **35**, p. 291. 1917) to be founded on faulty experimental methods, while Phillips (*Bot. Gaz.* **69**, p. 168. 1920) has shown fairly conclusively that no differences occur in the two sides of the stimulated organ, either in water content, or titration acidity, or hydrion concentration, or catalase activity, or sugar content, or percentage of nitrogenous substances.

charged particles which become redistributed when the organ is displaced. Then, if the obvious is admitted, and the root is taken as acidic and the stem as relatively alkaline, these particles must move *upwards* in both organs, not downwards; otherwise the current would pass in the other direction both in stem and root, and the stem would *normally* grow down, as it does practically every day in our laboratory *under the reversing action of excess of carbon dioxide*[1]. If, however, it can be shown that starch grains or other heavy bodies in the cell aid in the upward movement of these other particles, or that such starch grains are electro-*positive* in *alkaline* media and electro-*negative* in acid media, then they may be correlated with geotropism, but this type of "amphoteric" electrolyte is as yet unknown to science.

As a contrast it is quite a logical deduction from the well-known influence of hydrion concentration on enzymic and other biochemical reactions[2], that the P_{H} of the protoplasm is important in cell processes. Haas[3], for example, writes: "The reaction of protoplasm is one of the most important factors of metabolism." But the further deduction that this hydrion differentiation is the cause of the difference in geotropic response in stem and root is admittedly only a very plausible theory; nevertheless the experimental evidence in its favour rapidly accumulates.

In concluding it must be pointed out that all the steps which are supposed to occur in geotropic response are capable of experimental demonstration, if they do occur, and it is this aspect of the theory and its applications which is now receiving attention. I would also like to express my gratitude to Professor V. H. Blackman for the kindly and helpful interest he has taken in the theory and for giving me this opportunity of dilating upon certain aspects of it which, like other points, received only brief notice in the original condensed account.

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April, 1921.

[1] See a forthcoming communication by Miss M. J. Lynn.

[2] See *The Determination of Hydrogen Ions* by W. M. Clarke, Baltimore, 1920; also I. Aggazzotti in *Archiv f. Entwicklungsmechanik*, **37**, p. 1. 1913; W. J. Crozier in *Jour. Gen. Physiol.* **1**, p. 581. 1919; and E. O. Schley in *Bot. Gaz.* **56**, p. 480. 1913.

[3] *Bot. Gaz.* **63**, p. 232. 1917.

THE GROUPING OF VASCULAR PLANTS

By MARGARET BENSON

In 1908 the writer reviewed in this journal (**7**, p. 143) the range of the sporangial (especially the microsporangial) apparatus of Vascular Plants. The suggestion was made that all the types borne on the sporophyte could be homologized and that, by accentuating the resemblances between synangia, sori, sporangiophores, half anthers and seeds, we should be better able to concentrate attention on their probable origin.

As it has been found impossible to extend the denotation of the term "sporangiophore" to cover so many differentiated types it will be clearer to employ a new term and that of "soroma" is now suggested. By "soroma" we mean the sporangial apparatus of the vascular plant *plus* the receptacle or stalk. The soroma of the Psilophytales already showed a considerable range of structure but it agreed in being borne on an axial-like arm of the thallus or plant body, and in being radially symmetrical. In the case of *Hornea*[1] the soroma shows a flattened apex and a central columella and on several occasions was found to branch.

These recent revelations as to the structure of the earliest known land plants have heightened the interest in the sporangiophore (soroma) as we can now interpret its stalk (receptacle) as homologous with the primal type of axis of radially symmetrical plants indistinguishable from Thallophyta. Such cases as *Sphenophyllum fertile* and the anomalous branching systems of the soromata (synangia) of *Tmesipteris* fall at once into line with the structures found in the Old Red Sandstone plants. Mrs Thoday's theory[2] of the axial nature of the pedicel of the so-called "sporophyll" of *Tmesipteris* is much strengthened and the two leaf-like lobes can now be safely interpreted as cladodified branches of this axis. Such primitive uninerved leaves may be called "Haplophylls." In this discussion we will accept the view that Haplophylls are also characteristic of the great group of Lycopodiales although in some species of *Sigillaria* we find a variant.

[1] Kidston and Lang, *Trans. Roy. Soc. Edin.* **52**, Part III, p. 614.

[2] Sykes, "Anatomy and Morphology of *Tmesipteris*." *Ann. Bot.* **22**, 1908, p. 81.

In the Sphenopsida we find leaves which are also probably cladodified axes but they show a definite trend towards a repeated dichotomy of the veins and in many cases a palmate type of segmentation of the leaf. For such simply elaborated primitive leaves the term "Meiophylls" is suggested.

In the Meiophyll the branching is always a dichotomy in one plane so that the leaf is strap-shaped or flabelliform. In the interesting cases of vegetative branches of *Sphenophyllum* bearing both laciniate and entire Meiophylls, the entire are found to be lower down on the axis. Apparently the earliest record of the Meiophyll is to be seen in *Hyenia sphenophylloides* Nathorst (Middle Devonian)[1] where the appendages are either simple or dichotomously branched. Such appendages may have given rise equally to the segmented and the non-segmented cladodified leaves of the later species of *Sphenophyllum*. The same range occurs in the pinnæ of the early Fern Meriphyte such as *Sphenopteris* and it is obvious that the Meiophyll is homologous with such pinnæ. Though certain Fern pinnæ show this type of venation the complete leaf involves greater complexity.

Pseudobornia exhibits, so far as the writer knows, the most elaborated leaf of the Meiophyll type. It would be interesting to secure structural material of this variant.

In the "cone scale" of the Sphenopsid *Cheirostrobus* we find both soromata (sporangiophores) and a segmented bract-like structure. The dorsiventral branching of the so-called "cone scale" trace in the cortex of the axis is not to be regarded as a branching of the leaf trace, but the branching of the common axis trace which on dichotomy in the dorsiventral plane gives rise on the ventral surface to sporangiophores (axial structures) and on the dorsal surface to the Meiophyll which proceeds normally to branch in a palmate manner. Thus the very antiquity and hence primitiveness of this remarkable cone, so magnificently described by Scott, really is at the root of its complexity.

There is yet a third type of leaf among the Vascular Cryptogams, namely the complex meriphytic leaf of the Ferns. This type has been fully discussed by Lignier and others whose theories were critically examined and accepted by Tansley[2] in 1908. The extraordinary resemblance between what we regard as the leaf of

[1] Arber, *Devonian Floras*. Camb. Univ. Press, 1920. Fig. 25.

[2] Tansley, *Lectures on the Evolution of the Filicinean Vascular System*, 1908. *New Phytologist*, Reprint, p. 2.

Stauropteris (no stem has so far been discovered) and the fertile branching system of axes of some members of the Psilophytales seems to add a still fuller justification for the view that the "frond" of Ferns has been evolved from a branching thallus by the appendicularization of a system of branches whether fertile or barren. For such leaves the term "Meriphylls" is here proposed, as Jeffery's "Megaphyll" includes the Meiophyll.

The soromata were involved and with the new source of nutrition, which the cladodification of the system of axes supplied, are found to have themselves undergone elaboration into synangia and sori.

Segmentation of the synangium followed first into equivalent parts as in the Simplices and later along so many different lines of descent, as shown by Bower, into the Mixtæ type of sorus. In no case do we find an exception to the law that among the Meriphylls the soromata are "taken up" upon the leaves as the writer expressed it in the 1908 "Sporangiophore" paper. In contrast to this we note that among the Sphenopsida the soromata more or less retain their independence of the leaf even though the vascular supply may be given off from the axis together with that of the leaf as in the cone of Calamostachys.

Relative antiquity of strobilus formation.

Turning now to a consideration of the relative antiquity of strobilus formation in the three groups Haplophylls, Meiophylls and Meriphylls respectively, we see that strobilus formation occurred at a vastly earlier epoch in the Haplophylls and Meiophylls than in the Meriphylls. In fact it has never been recorded among the Filicales which are the only Cryptogamic representatives of the Meriphylls and was only attained relatively late by their seed-bearing congeners.

This fact may be correlated with the limitation of the branching of the originally appendicularized constituents forming the "cone scale"—only axes of the second or third order obtaining. In the Psilotales it is possible that the very frequent anomalies of *Tmesipteris* indicate that the telescoping down of the soromata-bearing axes to that now regarded as the normal may be comparatively modern. To sum up: in the character of the leaf, in the insertion of the soroma and in the date of strobilus formation we have characters distinguishing three groups of Vascular Cryptogams.

Let us now turn to the Spermophyta.

There is no group of seed plants with a universally uninerved leaf constructed on the plan of the Haplophylls.

A single vein occurs in some Conifers but the leaf trace is generally at least dual and leaves of different species of the same genus may have one vein or a trace that segments palmately as in species of *Podocarpus* and Araucaria. There is ample evidence that the leaf of the Cordaitales, Ginkgoales and Coniferæ falls within the Meiophyll type.

In *Podocarpus* each of the pair of cotyledons has two bundles, and the generally accepted interpretation of polycotyledony in the Conifers is that it is due to segmentation of an original pair. Ample evidence of this is given in the papers by T. G. Hill and E. de Fraine, I to III "On the Seedling Structure of Gymnosperms[1]." Not only the cotyledons of *Ginkgo* but all the foliage leaves are more or less lobed and this lobed, flabelliform leaf was especially characteristic of the ancient type of Ginkgoales called *Baiera*[2].

In the Cordaitalean circle of affinity there is no example known of a leaf with the veins branching otherwise than in the dichotomizing palmate method found in Meiophylls. It appears to the writer that such uniformity points to an important ancestral resemblance and probable affinity between the Sphenopsida and this ancient group of Families.

Let us turn now to the consideration of the insertion of the soroma and deal first with the megasoroma or seed. We find as pointed out in the discussion of the subject in the 1908 paper, "The Sporangiophore," we are possibly "dealing with plants which have never had their 'sporangiophores' taken up upon leaves and that, in fact, they are constructed in this respect upon the Equisetal plan where the sporangiophores are merely associated with bracts[3]."

This view has been adopted tentatively by Sahni in his recent review of the entire Gymnospermous series appended to his Monograph on *Acmopyle Pancheri* Pilger[4]. He shows there are two great divisions based primarily upon the manner in which the seed is borne, whether upon the leaf, or directly upon the axis. These two divisions he calls the Phyllosperms (leaf borne seeds) including the Cycadales and Pteridosperms, and the Stachyosperms (stem borne seeds) including the Cordaitales, Ginkgoales, Taxales and Coniferales.

[1] Hill and de Fraine, *Ann. of Bot.* 22, p. 689, and 23, pp. 189 and 433.

[2] See Seward's *Fossil Plants*, 4, pp. 1–60, where the Meiophyll type of leaf is well illustrated.

[3] *Loc. cit.* p. 149.

[4] Prof. Birbal Sahni, *Phil. Trans. Roy. Soc. Lond.* Series B, **210**, pp. 299–302.

He thinks there is strong negative evidence against the view that a sporophyll of the megaphyllous type had been originally present and has been lost but he concludes that the meagre positive evidence at present available is distinctly in favour of a common megaphyllous (meriphyllous) origin for the Cordaitales and Pteridosperms. It is this view that the writer wishes to counter. It is to her incredible that such ancient plants as *Cordaites* could have retained a catkin-like brachyblast which in its entirety might be regarded as homologous with the meriphyll of a Zygopterid Fern and that the parts really represent obsolete meriphytes.

In turning to the insertion of the microsoroma or pollen-bearing apparatus we seem to have secured new light from the comparison of the so-called "stamen" of *Cordaites, Taxus,* etc., with the sporangial apparatus of the Psilophytales. In both, the soroma is radially symmetrical and terminal on a simple stalk-like body. Those of the older members of Ginkgoales appear to resemble *Cordaites*. We have instances carefully worked out of the abortion of certain sporangia of the terminal cluster in *Ginkgo*[1] giving the dorsiventral type of *Ginkgo biloba*. The same phenomenon occurs in the passage from the radial symmetry of *Taxus* to that of the dorsiventral symmetry of *Torreya*[2] and *Cephalotaxus*. Such changes prepare us for the type found in Araucariaceæ and the more or less peltate form found in *Juniperus* and other Conifers. The Psilophytales prepare us for a transition from a radially symmetrical axial structure to a lamella. It seems to the writer to be reading complexity into simplicity to fail to accept the microsoromata and the megasoromata (seeds) as inserted directly upon axes. If this is recognized to be the universal condition in Sahni's Stachyosperms to what does the condition point? The Stachyosperms are not members of the same series as the Ferns, nor of the Pteridosperms, Cycadophyta nor Angiosperms. They are Meiophylls and not Meriphylls—to use the nomenclature of the earlier part of this discussion. They probably have some kinship in the remote past with the Cryptogamic Meiophylls and their resemblances to Cycads in their seed must be due either to the seed having originated before the distinctive types of foliage leaf were differentiated or possibly are due to homoplasy.

Sahni[3] and Sprecher[4] have shown that the seed of *Ginkgo* has

[1] A. Starr, "The 'Microsporophylls' of Ginkgo," *Bot. Gazette*, p. 134. 1910.

[2] Coulter and Laud, "Torreya taxifolia," *Bot. Gazette*, p. 159. 1905.

[3] Sahni, "On Certain Archaic Features in the Seed of Taxus," etc., *Ann. of Bot.* 34, p. 117.

[4] Sprecher, *Le Ginkgo biloba* (Genève, 1907).

close resemblance to the Cordaitalean and *Taxus* type, and possibly if we knew the history of the Cycad seed we could show that the resemblance to a Stachyosperm seed is the result of relatively recent convergence.

Further evidence in support of the original Meiophyll character of the leaves in Conifers is their early formation of a strobilus. The catkin of *Cordaites* is a strobilus and this strobilus or reproductive brachyblast (cf. *Taxus*) is regarded by the vast majority of morphologists at the present day as persisting in the form of the ovuliferous scale of the Abietineæ and in a more or less disguised form in the ligule of the "cone scale" of Araucarineæ where the one seeded character of the brachyblast is supposed to have facilitated a closer degree of fusion.

If one contrasts this early strobilus formation with that found among the Meriphylls where the earliest recorded case of strobilus formation is in the Triassic, we see how improbable as well as unnecessary it is to withhold credence from the view that the Stachyosperms are Meiophylls. It is for this reason they are entered as Meiophylls on the accompanying diagram on p. 89.

CONCLUSION.

The view that the Cordaitales had megaphyllous ancestors and that as a corollary the absence of sporophylls was due to reduction, is so widely found in botanical literature that it seems gratuitous to give any references. The view that the Araucarineæ belong to a distinct race from the Fern-Cycad alliance so ably reasoned out by Seward and Ford[1] in 1906 was still adhered to by the former in 1919[2] in the account of recent Coniferæ in his *Fossil Plants*. In this account he expresses doubt as to the brachyblast origin of the ovuliferous scale even in Abietineæ. The grounds for his view differ widely from those advocated in this paper as to the affinity of Coniferæ, for the presence and character of the reproductive brachyblast is here largely relied on as evidence of the independent origin of the Stachyosperms. It should be noted that Prof. Seward has never limited the suggested source of the Coniferæ to the Lycopods but again and again pointed out their resemblances to *Equisetum* and *Cheirostrobus*. In the Discussion at the Linnean Society[3] in 1906 it was obvious that more support would have been

[1] Seward and Ford, *Trans. Roy. Soc. Lond.* Series B. **198**.

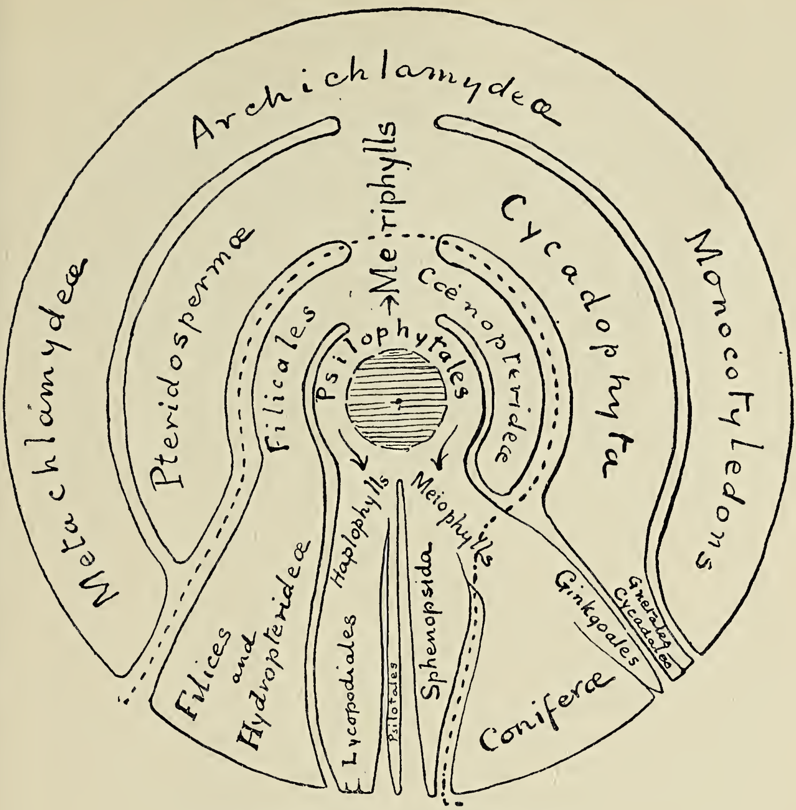
[2] Seward, *Fossil Plants*, **4**, p. 117.

[3] *New Phytologist*, **5**, "Discussion on the Origin of Gymnosperms."

given to Prof. Seward's view if the Lycopodiales had not been regarded as the alternative to the Fern-Cycad alliance.

Finally the writer wishes to express her full appreciation of the difficulties of the problem. They have however been probably aggravated by a too facile acceptance of an affinity between Coniferæ and Gnetales. The latter group is regarded by the writer as a vestigial remainder of the Cycadophyta which instead of "magnifying the office" of the carpellary leaf (megasporophyll), as happened in Angiosperms, reduced it until it became obsolete. The Gnetales are probably a comparatively recent group, for there is no record of the Cycadophyta until the Triassic. As in the Cycadophyta we have in the Gnetales ample evidence of a micro-sporophyll and of a meriphyll type of foliage leaf, for both in *Gnetum* and *Welwitschia* we find reticulate venation and even a pinnate type in the cotyledon of the latter. On such grounds as these the Gnetales are entered in the accompanying diagram as surviving members of Cycadophyta.

A warning note may be given with respect to the diagram. It is not intended to denote the relative dominance of the different groups in past epochs for there can be little doubt that the Stachyosperms were more abundant in the mesozoic times than even the Cycadophyta. The diagram and indeed the whole of this discussion arose in connection with an attempt to discuss the possibility of securing a logical sequence of Families of Vascular Plants for practical purposes. (See the "Note on a Numerical Sequence of Plant Families," p. 90.)



DESCRIPTION OF THE DIAGRAM.

The periphery of the diagram represents the end members of three evolutionary series, the Haplophylls, the Meiophylls and the Meriphylls, and, very roughly, their relative dominance at the present time.

All Families that fail to reach the periphery are extinct.

All Families outside the dotted line are spermophytes.

The circle in the centre, which is hatched, represents the pre-land-plants which, after Church, we are learning to call Thalassiophyta.

The annulus immediately surrounding this circle represents the earliest known vascular plants which may at present be identified with the Psilophytales of Kidston and Lang. From these proceed races with at least three types of appendicular, photosynthetic organs. It can be seen that the Haplophylls produced no seed plants; the Meiophylls are regarded as having given rise to the Sphenopsida, Cordaitales, Ginkgoales and Coniferæ; the Meriphylls are the successful races, giving rise to the Ferns, the Cycadophyta, the Gnetales and the Angiosperms.

NOTE ON A NUMERICAL SEQUENCE OF PLANT FAMILIES

In a recent number[1] of this journal a plea is put forward for a linear series of families of Vascular Plants. The fossil groups are not to be included, i.e. are not to have numbers assigned to them (*loc. cit.* p. 270) which is in harmony with the Botanical Garden outlook of the paper. Certain suggestions are made for the construction of such a series in a table, *loc. cit.* p. 269. As discussion is invited, I am venturing to make a few suggestions. A numerical sequence of families would certainly be useful from the point of view of economy of space in labelling museum specimens and living plants in a Botanical Garden. With a key to the family numbers, which Gundersen estimates at about 300, such labels, with the name of the species added, might be a great boon to students. Gundersen desires the sequence to be the result of general consideration "something like an inventory of facts which appear to have a bearing on family sequence." He is aware that the characters used in determining evolutionary sequence "are in nearly all cases very different from those by which plants are identified" and presumably would be prepared to have the Hydropterideæ broken up and one family associated with Schizeæaceæ and the other with Hymenophyllaceæ.

But even then this ideal seems difficult to secure for a single linear series. If we omit all the fossil groups the linear series will run more or less at right angles to the radial series which indicate the evolutionary series.

As, however, Gundersen obviously thinks the arrangement of the families in a numerical sequence should be on as natural a basis as possible I would suggest that it is of the first importance to determine the larger groups. In a paper in the current number of this journal I have discussed this question and have drawn up a diagram expressing the results to which I come. If this meets with his views let him record around the periphery of this diagram the 300 families to which he refers, locating them on that part of

[1] A. Gundersen, "Plant Families: A Plea for an International Sequence." *New Phyt.* **19**, p. 264. 1920.

the periphery which is allocated to their corresponding major group. For Ferns I should advise a reference to Prof. Bower—for the Conifers there is at present very little consensus of opinion. The three families of Lycopodiales and one family each of Psilotales and Sphenopsida will offer no difficulty. It will be seen that if the sequence follows the periphery it will be only a formal list in which sometimes consecutive numbers are applied to nearly allied families and sometimes to families exceedingly remote from one another in affinity, as is the case when one passes from the Haplophylls to the Meiophylls, and thence to the Meriphylls. A reference must be made to the accompanying paper for definitions of these terms and for an explanation of the diagram.

If these suggestions are of little service, at least they will show how remote botanical problems (even the morphological) are from solution.

M. Benson.

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PERMEABILITY

By WALTER STILES

CHAPTER III

SURFACE PHENOMENA

THE most obvious way in which the surface differs from the body of a liquid is in its behaviour as a thin stretched skin. This is most familiarly exemplified in the behaviour of films of soap solution.

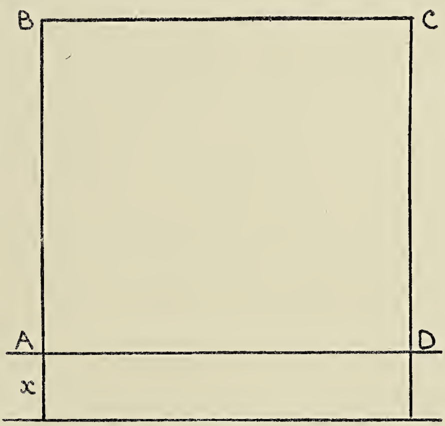

Fig. 1.

For instance if the rectangle enclosed by the wire frame *ABCD* (fig. 1) is occupied by a thin film of soap solution terminated at its lower edge by the wire *AD* which can move freely along the vertical wires *AB* and *DC*, the film will tend to contract and it is

necessary to attach a definite weight to AD in order to keep it in position.

The surface is thus the seat of special forces. How these come to be present can be understood from the following considerations:

In the mass of the liquid we have an enormous number of molecules, each one of which is surrounded on all sides by numbers of other similar molecules uniformly distributed round it. The mutual attraction of the molecules therefore results in nothing more than keeping them pressed together, the pressure on any particular molecule being uniform in all directions. By the force of cohesion the liquid particles are kept together, and do not tend to separate as in the case of a gas. At the surface of the liquid the state of affairs is different. A molecule at the very surface is subjected to the attractive force of molecules in the interior of the liquid, but there is no similar balancing force at the exterior. This means that the surface layer is subjected to an inwardly directed pressure at right angles to the surface, a pressure which decreases rapidly in the direction away from the surface as the cohesive force of the molecules is more uniform in all directions.

This inwardly directed pressure at the surface has two results. In the first place as all liquids are compressible to a small extent the surface layer of liquid will be compressed; in the second place as all the molecules at the surface are pressed towards the interior the surface will tend to contract to its smallest possible area.

So far the surface has been spoken of as if there were nothing outside the liquid. As a matter of fact there must always be some substance in contact with the liquid. Now a force of attraction called adhesion exists between molecules of different substances, consequently the actual inwardly directed pressure at the surface is the result of the difference between the pressure due to cohesion of the liquid and that due to adhesion between the liquid and the external medium. Only when the cohesion and adhesion are equal the pressure will be zero.

We thus see that the surface is in a state of tension by which it tends to reduce its area to the least possible. The *surface tension* of a liquid is defined as the force acting on unit length in the plane of the surface. From what has already been said it is clear that the surface tension depends not only on the nature of the liquid itself, but also on the medium with which it is in contact. The surface tension for instance of the surface water/air will not have the same value as the surface tension of the surface water/alcohol. When the

surface tension of a liquid is spoken of it is generally the surface tension of the liquid against air that is meant.

The surface tension of a liquid, besides depending on the nature of the liquid and on the medium with which it is in contact, also depends on the temperature.

It is outside the scope of this work to describe the different methods used for the measurement of surface tension. For these reference may be made to standard text-books of physics (*e.g.* Poynting and Thomson, 1905; Winkelmann, 1908). The principles of the more ordinary methods consist respectively of: (1) the measurement of the height to which liquid will rise in a capillary tube; (2) the measurement of bubbles and drops (Quincke); (3) the measurement of the size of drops of the liquid as it issues from a narrow tube; (4) measuring the least pressure necessary to force bubbles of air from the orifice of a narrow tube dipping in the liquid (Jaeger); (5) the determination of the deformation produced in the cross-section of a stream of liquid issuing from an elliptical orifice; (6) forcing a stream of the liquid upwards through a small orifice and measuring the height to which it will rise; (7) the determination of the velocity with which waves travel over the surface of a liquid (Rayleigh); (8) observations of oscillations of a spherical drop of liquid (Lenard, 1887). These and other methods will be found described in physical text-books.

The following table shows the surface tension of a number of liquids in contact with air, as determined by the capillary method, at 20° C.

TABLE I

Surface tension of certain liquids in contact with air at a temperature of 20° C.

Substance	Surface tension in dynes per cm.
Water	72·53
Acetic acid	23·46
Ethyl alcohol ...	22·03
Ether	16·49
Chloroform	25·88
Olive oil	35·4

In Table II are given the surface tensions of a number of liquids against different substances.

TABLE II

Values of the surface tension of the same liquid against different substances at 20° C. (Data from Quincke)

Liquid	Surface tension in dynes per cm. against air	water	mercury
Water	80·97	0	41·77
Mercury ...	53·98	41·77	0
Alcohol ...	25·49	—	39·93
Chloroform ...	30·61	29·52	39·93
Olive oil ...	36·88	20·56	33·54

The values given in this table are due to Quincke. His determinations are now generally regarded as somewhat high, and the figures given in Table I for surface tensions against air are lower in all cases than those found by Quincke. This does not affect the comparison of the surface tensions against different substances.

With increase in temperature the surface tension diminishes. Eötvos (1886) has propounded the following relation between surface tension and temperature

$$\frac{d\,(\sigma v^{\frac{2}{3}})}{d\theta} = -\,2{\cdot}1$$

where σ is the surface tension, v the molecular volume (*i.e.* molecular weight/density) and θ the temperature whatever the value of θ and whatever the substance. From this equation can be calculated the value at which the surface tension becomes zero; calculation shows this temperature differs very little from the critical temperature. (Poynting and Thomson, 1905.)

Since the surface of a liquid is in a state of tension, it follows that when it contracts energy is released, and conversely, when a surface is increased work has to be done against the tension. Consequently the surface is the seat of energy. Referring to the example of the soap film in fig. 1, since the surface tension is the force exerted by unit length of the surface, and since there are two surfaces to the film, the weight required to keep the wire AD in equilibrium must be $2\sigma . AD$.

Now if the film is stretched so that BA and CD are increased in length by a quantity x, the work done in stretching the film is

$$2\sigma . AD . x$$

or $2\sigma\omega$ where ω is the area by which the surface has been increased.

Consequently the potential energy of a surface is the product of the surface tension and the area. This quantity is called the *surface energy.*

It has been pointed out (Helm, 1887; Bayliss, 1915) that in general energy can be regarded as the product of two factors, an "intensity factor" of the nature of a force, and a "capacity factor" which is always a measure of size, such as mass, volume, area, length, etc. In the case of electrical energy for example, the intensity factor is difference of potential and the capacity factor strength of current. The capacity factors of two systems add together and the sum gives the capacity factor of the whole, the intensity factors cannot be added together. For instance in the case of heat, where the intensity factor is temperature, the sum of the temperatures does not give the temperature of the whole system. Differences in the intensity factor always tend to disappear. Thus two bodies in contact tend to come to the same temperature, or to the same potential. On the other hand there is as a rule no tendency for differences between capacity factors to disappear.

In the case of surface energy, the intensity factor is obviously the surface tension, and the capacity factor the area of the surface.

Now it is an important law of energetics that free energy always tends to reduce itself to a minimum, and hence the surface energy of a liquid will tend to diminish whenever this is possible. In most cases it is only the intensity factor which is capable of alteration to bring about reduction in the free energy, but in the case of surface energy both the intensity and capacity factors tend to diminish to the minimum possible value, that is the surface tension will reduce itself whenever possible and the surface will contract to the smallest possible. A reason for this has already been given in this chapter.

The tendency for surface tension to diminish is probably a principle of great importance in regard to permeability. In the case of two pure and immiscible liquids in contact there is no possibility for the surface tension to be reduced as this is a function of the nature of the liquids and the temperature. The case of a liquid that contains more than one component requires more consideration. In this case if the surface tensions of two components in the pure state are different, the surface tensions of mixtures of the two are intermediate between those of the pure liquids. Thus in the case of mixtures of ethyl alcohol and water, if the surface tension of pure water against air is taken as unity, that of ethyl alcohol against air is only 0·302. The curves in fig. 2 show how the addition of various alcohols to water lowers the surface tension of the latter. So far however it has not been possible to express the exact relationship

between surface tension and concentration of a solution algebraically.

In the case of a solution of ethyl alcohol in water the surface tension will obviously be reduced if the concentration of alcohol in the surface is raised. According to the principle first enunciated by Gibbs (1878, 1906) and emphasized by J. J. Thomson (1888), there will thus be a tendency for the alcohol molecules to migrate to the surface, so that the concentration in the surface layer is greater than

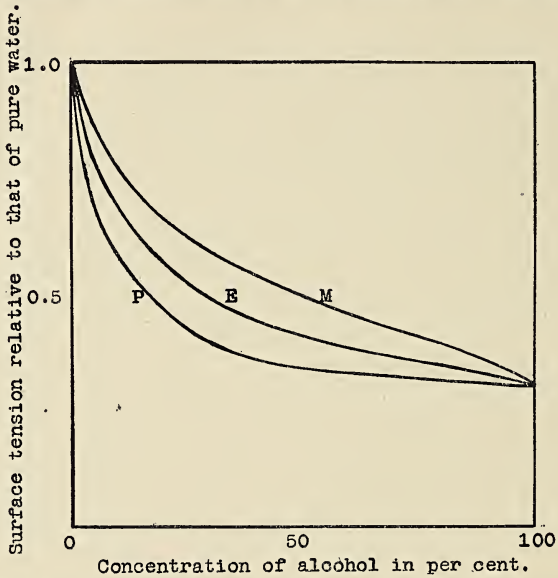

Fig. 2. Curves showing the relation between surface tension against air and composition of solutions of methyl (M), ethyl (E), and isopropyl (P) alcohols in water.

in the rest of the liquid. Opposing this tendency is that of the dissolved substance to diffuse from a place of higher to one of lower concentration. An equilibrium condition will thus be reached where these two opposed tendencies balance one another. It has been shown by Gibbs that when equilibrium is attained

$$\Gamma = -\frac{C}{RT}\cdot\frac{d\sigma}{dC}$$

where C is the concentration of the solute in the bulk of the solvent, Γ the excess of solute in the surface, $\frac{d\sigma}{dC}$ the rate of change of surface tension with concentration of the solute, T the absolute temperature, and R the gas constant.

The accumulation of a dissolved substance at the surface forming the junction between two phases is called *adsorption*, and when it takes place purely as a result of the mechanical surface tension it is called *mechanical adsorption*.

It will be observed that accumulation of solute in the surface layer can only take place if the dissolved substance lowers the surface tension of the solvent. If on the other hand the dissolved substance should bring about an increase of the surface tension, the concentration of the surface layer will be less than that of the rest of the solution, and negative adsorption will result.

Attempts to verify the formula of Gibbs have been made by Lewis (1909) and by Donnan and Barker (1911) and an approximate agreement with the formula has been obtained in some cases. In the following table are shown the values found experimentally for Γ compared with the values obtained by determination of $\frac{d\sigma}{dC}$ and subsequent calculation from Gibbs's equation.

TABLE III

Values of Γ found and calculated. (Lewis)

Substance	(In gm. per sq. cm.) found	calculated
Sodium glycocholate	5×10^{-6}	7×10^{-8}
Congo red	$3{\cdot}7 \times 10^{-6}$	$1{\cdot}1 \times 10^{-7}$
Methyl orange	$5{\cdot}5 \times 10^{-6}$	$1{\cdot}2 \times 10^{-7}$
Sodium oleate	10^{-6}	10^{-8}
Sodium hydroxide	$1{\cdot}5 \times 10^{-7}$	$7{\cdot}5 \times 10^{-9}$
Caffeine	$3{\cdot}7 \times 10^{-8}$	$2{\cdot}4 \times 10^{-8}$
Sodium nitrate (kation)	$2{\cdot}5 \times 10^{-8}$	$4{\cdot}5 \times 10^{-9}$
Potassium chloride (kation) ...	5×10^{-8}	$1{\cdot}7 \times 10^{-9}$
,, ,, (anion) ...	10^{-9}	$1{\cdot}6 \times 10^{-9}$
Barium chloride (anion)	not $> 10^{-8}$	$1{\cdot}6 \times 10^{-9}$
Copper chloride (anion)	$3{\cdot}5 \times 10^{-8}$	2×10^{-9}
,, ,, (kation)	2×10^{-8}	2×10^{-9}

Lewis concludes that caffeine probably obeys Gibbs's Law quantitatively. In other cases the values found experimentally are always greater than those obtained by calculation with the exception of the anion of potassium chloride. Lewis thinks that some irreversible phenomenon such as gelatinisation at the surface may be the explanation of the discrepancy. As will be shown later in this chapter electrical phenomena are often present at a surface which add to the complexity of the matter.

Any substance dissolved in water lowers its surface tension against a solid or immiscible liquid, and this is usually the case also when

the solution is in contact with a gas. There are however some substances which increase the surface tension of water against air, among which are most inorganic salts, although these lower it at the interface between water and oil (Lewis, 1909).

An anomalous case of surface concentration is met with in the case of sugars. It appears that these substances in solution do not lower the surface tension of water. Nevertheless they are adsorbed at the surface to a slight extent (Adler and Hertzog, 1908; Hertzog, 1908; Rona and Michaelis, 1909). The explanation of this phenomenon offered by Rona and Michaelis is that the surface layer is in a state of compression (see p. 94) and the solubility of the dissolved substance is greater in this compressed layer than in the bulk of the solution.

In many cases the presence of the adsorbed material in the surface film of a liquid will increase the viscosity of the liquid at the interface. This may account for the formation of the rigid membranes observed by Ramsden. Similar membranes have also been obtained by Metcalf (1905) and Zangger (1908).

As we have seen in Chapter II we are concerned in the living cell with a decidedly viscous substance, and we can thus understand how the cytoplasmic "membrane" when damaged is immediately reformed, as has been often observed, *e.g.* by Chambers (1917) and Seifriz (1918).

Adsorption is in general a reversible process. In the case of such viscous fluids as solutions of proteins, soaps and bile acids, on the contrary, the process is irreversible.

Equations connecting the amount of adsorption at equilibrium with the concentration have been obtained empirically. Among the better known of these are those due to Küster (1894) and Schmidt (1894); the relation is most usually expressed in the form due to Freundlich (1909), which is

$$\frac{x}{m} = kC^{\frac{1}{p}}$$

where x is the mass of substance adsorbed by a mass m of the adsorbent, C is the concentration of the solution after adsorption has reached equilibrium, and k and p are constants. The value of p varies between 1·25 and 5, but it is very commonly about 2. This equation it will be observed may be written in the form

$$\log\left(\frac{x}{m}\right) = \frac{1}{p}\log C + K.$$

If then the logarithm of the amount of material adsorbed is plotted against the logarithm of the concentration at equilibrium, straight

lines will be obtained if the adsorption equation holds; this is shown to be approximately the case.

It follows from the adsorption equation that as the concentration of the solution increases the quantity adsorbed increases, but the quantity relative to the concentration decreases. For example, if finely divided charcoal is added to solutions of substances, adsorption generally takes place at the surface of the charcoal. Now if charcoal is added to a solution of acetic acid in water, when the concentration of the acetic acid at equilibrium is 0·018, the quantity adsorbed per unit mass of adsorbent is 0·467; when the equilibrium concentration is 2·79, the quantity adsorbed per unit mass of adsorbent is 3·76. That is, although $\frac{x}{m}$ in the adsorption equation has increased from 0·467 to 3·76, its value relative to the concentration of the solution, has decreased from 26 to 1·35.

As surface tension decreases with rise in temperature so adsorption also is less the higher the temperature. As the adsorption at a temperature $\theta + 10$ is thus a fraction of what it is at θ, adsorption has a *fractional temperature coefficient*, if the temperature coefficient of a process is regarded as the number by which the value of the process at one temperature has to be multiplied in order to give the value of the process at a temperature 10 centigrade degrees higher. The temperature coefficient is then generally denoted by the symbol Q_{10}. When the process, as in the case of adsorption, is lessened with rise of temperature, the temperature coefficient is less than unity. Such processes are often spoken of as having a *negative temperature coefficient*. This is not necessarily a misuse of the term negative, for by "temperature coefficient" is sometimes understood the quantity, or a multiple or fraction of a quantity, which has to be added to the value of a process for a rise of 1° C. This temperature coefficient is often denoted by the symbol α. It is unfortunate that the term "temperature coefficient" should be used in these two senses.

It must be noted that although adsorption decreases with rise of temperature, the rate at which adsorption is brought about increases. This is due to the fact that the rate of adsorption must depend on the rate at which the adsorbed substance can diffuse through the medium containing it. It is therefore to be expected that the rate of adsorption would have a temperature coefficient not far different from that for rate of diffusion, and this has been shown by Bayliss (1911) to be the case with adsorption of congo red by filter paper.

So far only pure substances, or solutions of one substance, have been dealt with. In the organism on the contrary we always have to deal with mixtures.

In general if there are two substances which can be adsorbed they displace one another to some extent. As the concentration of one of the substances increases, more of it is adsorbed and displaces the other to a greater extent, but relative to the concentration the amount of displacement decreases with increasing concentration. An exception to this is found in those viscous substances which tend to form rigid membranes at the surface. The presence of a viscous solute has no influence on the adsorption of a solute of low viscosity.

Another peculiarity of such substances is that the extent of adsorption depends not on their concentration, but on the absolute amount present. It is not clear how far the peculiar properties of such substances are due to high viscosity, low diffusivity or colloidal nature. Sugar as is well known considerably increases the viscosity of water, but the adsorption of sugar follows the ordinary laws and is reversible.

So far we have considered the consequences of the tendency of surface tension to reduce itself to a minimum. A few words are now necessary regarding the tendency of the area of the surface to diminish as far as possible. This is illustrated by the fact that liquids free from external forces always take up a spherical form, while if a liquid is divided into droplets scattered through another liquid of the same density, and with which the first liquid is immiscible, the droplets tend to unite into larger ones and finally into one single sphere.

In the case of living matter of a gel nature, however, we have a substance which possesses a certain amount of rigidity. Any change in form of droplets of such a substance will therefore be opposed by the resistance offered by the rigidity of the substance to change of shape, and a condition of equilibrium will be reached when these two tendencies are equal.

The tendency of surface tension in gels is therefore to bring about the coalescence of separated droplets. This union is called agglutination when microscopic particles coalesce into particles visible with the naked eye, and coagulation when the particles that unite are ultra-microscopic or very finely microscopic. Agglutination and coagulation may therefore be produced either by an increase in surface tension or by a decrease in rigidity of the dispersion medium.

So far we have considered the surface effects which are attributable to purely mechanical phenomena. The conditions at surfaces are however actually often more complex than has so far been indicated owing to the very general presence of electrical forces at the interface between two phases.

We know for instance that if a metal is immersed in a solution of one of its salts a difference of potential between the metal and solution results, and that the existence of this potential can be explained by the tendency of metallic ions to pass into solution. When this takes place the metallic ions give to the solution a positive charge, leaving the metal plate correspondingly negatively charged. The solution of the metal can therefore only proceed until the mutual attraction due to the difference in potential is balanced by the tendency of the metal to go into solution; *i.e.* by the electrolytic solution pressure of Ostwald which is proportional to the ratio between the concentrations of atoms in the metal and ions in the solution. The difference of potential is given by the expression

$$RT \log \frac{P}{p}$$

where P is the electrolytic solution pressure, p the osmotic pressure of the ions in solution, T the absolute temperature and R the gas constant.

The same considerations hold for hydrogen as for a metal and are the basis of the well-known electrometric method now so universally employed in physiology for measurement of hydrogen ion concentration.

In the case of the surface between a solid electrolyte and its solution similar considerations hold, though the matter is complicated by the presence of two ions. In this case the potential at the interface between the solid and liquid phases is given by

$$RT \log \frac{P^{\cdot}}{p^{\cdot}} \left[= RT \log \frac{p'}{P'} \right]$$

where $P^{\cdot}$, P' are the electrolytic solution pressures of the kation and anion respectively and $p^{\cdot}$, p' are the osmotic pressures of kation and anion in the liquid phase.

In general, for the potential difference due to one ion at the interface between any two immiscible phases, we have for the value of the potential the expression

$$\frac{RT}{nF} \log \frac{c_1}{c_2} + K$$

where c_1 and c_2 are the concentrations of the ion in the two respective phases, n the valency of the ion, F the electric charge of a monovalent gram-ion, and k a constant. It is outside the scope of this work to describe how these formulae are derived; those interested should consult the original work of Nernst (1889, 1892) and Haber (1908) and the general account of electrical phenomena at surfaces given by Michaelis (1914). For the application of these formulae to biological phenomena reference may be made to the papers of Beutner (1912, 1913) and Loeb and Beutner (1912).

It should be emphasized that the difference of potential (phase potential) arises from the unequal partition coefficients of the two ions between two phases, and is not connected with the different mobilities of the two ions. A difference of potential due to this latter cause (diffusion potential) arises when two solutions containing the same ions but in different concentrations come into contact. Diffusion takes place and if the mobilities of the two ions are different one ion will diffuse faster than the other and a difference of potential will thus result.

It appears however that the sign of the charge should be the same in whichever of the two ways the difference of potential arises, for in the latter case the solution takes the charge of the more mobile ion and in the former case it takes the charge of the more soluble one, and it appears that the more soluble ions are also the more mobile (Michaelis, 1914). Probably the electric charge at most surfaces can be accounted for in one of the preceding ways, but there are cases, as for instance that at the surface of aniline in contact with water (Ellis, 1912) where the aniline is negatively charged, although one would expect it to be positively charged as it feebly dissociates into the slightly mobile aniline ion $C_6H_5.NH_3$ and the very mobile hydroxyl ion. Although explanations have been offered of such cases (Lewis, 1910) the problem cannot be regarded as solved.

We may now pass on to a consideration of how adsorption is affected by electrical phenomena.

In the first instance we may consider a case of an electrolyte partly dissociated into its constituent ions. There will then be in solution the kation, the anion and the undissociated molecule all with their characteristic constants in regard to the adsorption equation, so that they tend to be adsorbed to different extents. Any difference in adsorption of the kation and anion must however be very slight as this would result in a potential difference between the surface and the interior of the liquid. An equilibrium position would

soon be reached where the force of attraction between the excess of oppositely charged ions would prevent any further separation. Such differences in potential due to inequalities of differently adsorbed ions are called *adsorption potentials* (see Freundlich, 1909).

The charge at a surface may itself be responsible for adsorption. By the principle that free energy will always reduce itself to a minimum, the electrical energy at a surface will tend to diminish whenever this is possible. Now if a surface is the seat of a negative charge, the deposition of any particle or ion carrying a positive charge will reduce the electrical energy of the surface, and such deposition will therefore tend to take place. That this is actually the case has been shown by Perrin (1904), Bayliss (1906), Lachs and Michaelis (1911) and others. For instance Bayliss has shown that a negatively charged surface such as that of filter paper will adsorb large quantities of an electropositive substance such as night blue, but only a trace of substance carrying a negative charge such as congo red. In some cases of such *electrical adsorption* the charge on the surface may actually be reversed; it seems likely that in these circumstances we are dealing with a complex effect in which both mechanical and electrical adsorption are involved.

Adsorption may obviously have an effect in regard to chemical reactions taking place at the surface. Thus if two substances which react together are adsorbed on the surface of a third, combination will take place on the surface of this third substance, which itself may remain unaltered. In a similar way reactions may take place if two substances mutually adsorb one another as in the case of barium hydroxide added to colloidal silica (van Bemmelen, 1910). A white substance is precipitated containing both substances, and from the mixture barium silicate slowly forms.

In such cases the active mass of reacting substances is the number of molecules adsorbed to the surface, and this number is proportional to the extent of the surface. Hence in such cases the rate of reaction is proportional to the surface. This is for example very generally the case in enzyme actions (see Bayliss, 1914).

Finally it must never be forgotten that all the phenomena of surfaces occur not only at the obvious surfaces of the cell, but throughout the colloidal substance of which the protoplasm is composed. Protoplasm is a heterogeneous system of more than one phase and throughout the system whenever there is a boundary surface between the disperse phase and the dispersion medium the surface phenomena described in this chapter must occur. A general

acquaintance is assumed here with the properties of colloids. Reference may be made to the works of Hatschek (1913), Taylor (1915), Bayliss (1915, 1918) and Wolfgang Ostwald (1909) in which colloids are treated from various standpoints.

OSMOTIC PRESSURE, ROOT PRESSURE, AND EXUDATION

By V. H. BLACKMAN

(With 3 figures in the text.)

The exudation of sap from the cut stem of a rooted plant is such a striking phenomenon that it is not surprising that many attempts have been made to elucidate the physics of the process. A number of the older workers attempted to explain the phenomenon on simple physico-chemical principles and recently Rowell (1918), and Priestley (1920) in this Journal, have again discussed its mechanism.

It is usually assumed that the osmotic pressure of the living cells of the root and stem play a main part in the production of root pressure, and it is usually recognised that one of the chief difficulties is the passage of water or a weak solution from the living parenchyma cells into the cavities of the dead wood-elements. Priestley accordingly suggests that the explanation put forward by Lepeschkin (1906) of the exudation of water by the sporangiophore of *Pilobolus* and by the multicellular epidermal hydathodes of the leaves of *Phaseolus* and other plants may be used to account for the passage of water from the living cells into the dead wood-elements. Since Lepeschkin's views seem to have been accepted by some other botanists, and have received the support of Bayliss by inclusion in his *Principles of General Physiology* (1918), it would seem worth while to consider them in some detail.

Pfeffer (1877), at the time that he was making his classical researches on osmotic pressure, was the first to deal critically with the mechanism of the exudation of fluid from living cells. He formulated three hypotheses: (1) that the plasma membrane develops unequal osmotic pressures in different parts of the cell; (2) that there

is an unequal distribution of osmotic material in different parts of the cell; (3) that osmotic material is present in the cell wall outside the membrane so that water is sucked out of the cell. The first hypothesis is obviously unsatisfactory, since it makes osmotic pressure a function of the membrane instead of the concentration of the solution. At the time, however, that Pfeffer was writing osmotic pressure was very vaguely conceived, so that the presentation of such a view by a worker of the competence of Pfeffer is hardly surprising. In a later publication Pfeffer (1890) recognised the physical fallacy involved in this view, and characterised his first hypothesis as "irrig."

The value of Lepeschkin's work on *Pilobolus* and *Phaseolus* lies in the very careful measurements which he made of the effect of various factors on the rate of exudation of water. When, however, he deals with the interpretation of his results he passes in careful review the three hypotheses of Pfeffer outlined above and makes a surprising decision in favour of the first scheme—that of a cell with a plasma-membrane of different osmotic pressures in different parts, no reference being made to the fact that *Pfeffer had himself rejected this scheme fifteen years earlier.*

It is clear that the permeability of the membrane can only affect indirectly the osmotic pressure of the solution which it encloses by controlling through exosmosis the concentration of the solution. The osmotic pressure developed with such a leaky membrane will thus depend only in part on the specific permeability of the membrane. Other important factors will be the original concentration and mass of the solute and the time during which exosmosis has continued. If the membrane is rigid the pressure first developed will be practically the same as if the membranes were truly semi-permeable. Lepeschkin further holds that not only has a *membrane* a specific osmotic pressure, but that directly that pressure is exceeded water begins to pass out through the membrane (*loc. cit.* p. 425). The same solution can thus at the same time be both in equilibrium with and not in equilibrium with water; or rather it can be on both sides of the equilibrium point at the same time!

Enough has probably been said to indicate that Lepeschkin's view, that the exudation of fluid by *Pilobolus* and *Phaseolus* is due to the osmotic pressure of the excreting cell together with the differential permeability of the two sides of the cell, is supported by arguments of such doubtful validity that it cannot be considered acceptable. It is perhaps the barricade of mathematical equations

with which Lepeschkin surrounds his discussion of exudation that has protected him from the criticism that might be expected. The only other criticism that has been met with is that of Höfler (1920), who remarks in a footnote: "Lepeschkin's Ausfuhrungen wonach der osmotische Druck der Zellen von deren Permeabilität abhangt scheint von theoretischen Standpunkt einer Revision bedurften."

Thoday (1918) has pointed out in this *Journal* how unsatisfactory is the usual presentation of the botanical aspects of osmotic pressure. For this the writers of text-books of physics and physical chemistry would seem in part responsible, for usually they do not sufficiently insist that osmotic pressure is the result of the tendency towards equilibrium between water and the solution, the absence of equilibrium being shown by the lower vapour tension of the solution as compared with that of water. The osmotic pressure of a solution is thus *an equilibrium pressure, i.e. the pressure which must be applied to the solution to bring it into equilibrium with water*[1].

To ascribe to the osmotic pressure of a given solution the responsibility for the exudation of water or of a weaker solution from that solution is certainly most unsatisfactory. Other pressures can be superimposed on osmotic pressure which may increase, decrease or even reverse it, but once osmotic pressure is recognised as an equilibrium pressure it is clear that it must always exhibit itself as a tendency to draw water into the solution, *i.e.* to bring about the absorption of water. Substances may pass out of the solution by diffusion if the membrane is permeable and so bring other forces into play outside the solution, or there may be other forces at work (such as electrical ones) which drive the solution out through the membrane, but such processes cannot be ascribed to the action of the osmotic pressure of the enclosed solution.

Since osmotic pressure is an equilibrium pressure it is obvious that by subjecting a solution to varying pressure it can be brought into equilibrium with—*i.e.* will neither give water to nor take water from—a solution of any concentration lower than that of the solution itself. It is easy then to appreciate that as a flaccid cell swells and the pressure of the cell wall increases the cell contents come into equilibrium with solutions of lower and lower concentration or osmotic pressure, and finally when the pressure exerted by the membrane is equal to the osmotic pressure of the cell contents the cell is in

[1] A very satisfactory treatment of osmotic pressure is that by E. W. Washburn, *An Introduction to the Principles of Physical Chemistry*. New York. 1915.

equilibrium with water. The osmotic pressure of the solution with which the cell is in equilibrium gives a measure—in terms of osmotic pressure—of the absorbing power of the cell[1] (Ursprung and Blum, 1916; Thoday, 1918).

Accepting the differential permeability of the upper and lower membranes of the sporangiophore of *Pilobolus* it may be compared with an artificial cell *A* (fig. 1), closed below by a perfectly semi-permeable membrane *B* and above by a membrane *C* which is slightly leaky, *i.e.* allows some of the osmotic material to diffuse out slowly. If such a cell is placed with its lower end in water, fluid will pass in,

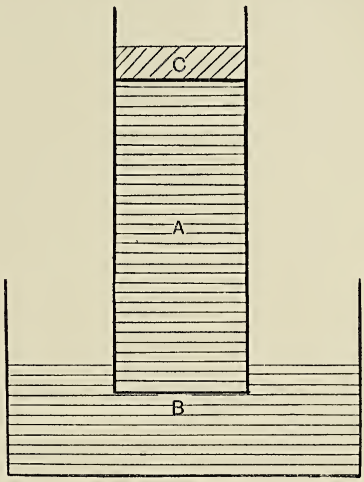

Fig. 1

and after a time the pressure exerted will equal the osmotic pressure of the contained solution. Water will then cease to enter, and the absorbing power of the cell will be zero. If now a drop of water be present above the upper membrane (*C*) osmotic substances will diffuse through the membrane and we shall have a weak solution above the cell. This solution will now have a higher absorbing power than the cell and so will draw water out of it. This loss will be immediately balanced by absorption through the lower membrane. The volume of the fluid at *C* will thus increase, *the force with which water is drawn into it depending solely on the difference of the osmotic*

[1] The absorbing power of a cell can be determined by finding the osmotic pressure of a solution which just does not alter the volume of the cell. This is the method used by Ursprung and Blum in their numerous measurements of the absorbing power of cells.

pressure of the fluids at C and at B, though of course the resistance of the two membranes will retard the rate of entry of the water. The osmotic pressure of the solution in *A* plays no part in the process, for *A* merely acts as a carrier of water and a reservoir of solute which can diffuse into the fluid above *C*.

In *Pilobolus* the excreted fluid is a weak solution containing no organic matter and with a concentration of mineral substances only one quarter that of the cell contents, so that unless the tension of the membrane comes into play the water from these drops will be drawn back into the cell—a difficulty by the way which Lepeschkin never meets. When the upper membrane of the sporangiophore becomes permeable some of the osmotic substances present in the cell sap will diffuse out into the water imbibed in the cell-wall. This weak solution would then draw water through the turgid cell in the manner just described for the model, and so the drops would be formed.

That drops of fluid might arise on the turgid sporangiophore of *Pilobolus* in this way seems clear, but the view that such a mechanism plays any important part in the actual process of exudation seems, on the other hand, very doubtful. The high temperature coefficient for exudation observed by Lepeschkin is rather against this view, though the effect might be due to the increased permeability of the protoplasm to water (see Delf, 1918). More definitely against the view is the fact that at a high temperature and under the action of alcohol the exudation may go on up to a point at which the turgor of the cells is markedly reduced, and it may even go on when the cell is partly plasmolysed by a 0·5 per cent. solution of NaCl. One would expect the exudation of fluid to stop before the turgor had been markedly reduced. The salt solution would certainly bring the absorbing power of the cell beyond the osmotic force of the drops (which is less than 0·35 per cent. NaCl), so that the continuance of the exudation, though at a diminished rate, is definitely against such a simple explanation of the mechanism. The process is probably a more complex one, depending on special energy relations of the living cell.

The hydathodes of *Phaseolus* and the secreting systems acting in root-pressure are essentially similar, but differ from *Pilobolus* in that the secreting cell or cells are separated from their water supply by a chain of intermediate cells. Now Lepeschkin claims that in order that water may pass to the apical secreting hairs of the *Phaseolus* hydathodes an osmotic gradient must exist with the apical secreting cells exhibiting the highest osmotic pressure; and Priestley appears

to assume such a gradient between the root-hair and the wood-elements. It has been pointed out in this *Journal* by Thoday[1] (1918), in an admirably clear and useful paper, that such a gradient is in no way necessary; all that is required in the chain of cells is a *gradient of absorbing power* with the highest absorbing power in the secreting cell; this might easily be consistent with a reversed *osmotic* gradient. Furthermore it may be pointed out that if the water supply is ample and there are no intermediate losses of water such a gradient will necessarily arise whatever the distribution of osmotic pressures.

If in fig. 2 we imagine that the root-hair, *A*, exposed to water has the highest osmotic pressure and the cells *B* to *E*, and the xylem vessel *F*, progressively lower pressures, water will still pass in from

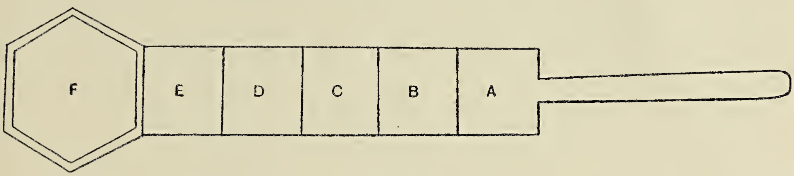

Fig. 2

A to *F*. For as *A* takes up water its absorbing power will tend to fall below that of *B*, when *B* will immediately take water from it, the absorbing power of *B* will then tend to fall below the osmotic pressure of *C*, and *C* will immediately take water from *B*, and so on; thus a gradient of absorption will arise. As the cells get turgid and cease to have any absorbing power, *F* will be able to draw water from outside *A*, *however low its osmotic pressure*, and the *force* with which water is drawn in will depend solely on the difference between the osmotic pressure of the contents of *F* and the osmotic pressure of the solution external to *A*. The osmotic pressure of the other cells can be neglected, though the resistance to water passage resulting from the interposition of these cells will reduce the rate at which water will pass from *A* to *F*.

The existence of an osmotic solution in the vessel *F* could be explained, as in *Pilobolus*, as a result of diffusion from *F* through the partially permeable membrane between the two. The accumulation of fluid under pressure in *F* would depend, as already stated, solely on the osmotic pressure of the solution in the vessel, and would

[1] Höfler (1920) has recently dealt with the water relations of the cell in a manner very similar to that of Thoday but somewhat more fully; he makes however no reference to Thoday's paper.

in no way depend upon the osmotic pressure in the adjacent living cells E, although such a dependence is usually assumed in theories of osmotic pressure. The objection to the assumption of such dependence may be put in another way—if the osmotic pressure of E is acting freely it would draw water back from F, if the pressure in E is opposed by the tension of the cell-wall it cannot exert pressure on the contents of F.

That the exudation of fluid from the open vessels of the wood could arise in this way seems clear, but just as in the case of *Pilobolus* it is very doubtful whether such a mechanism plays any part in the "bleeding" of cut stems. As with this mechanism the driving force depends on the concentration of the solution in the vessels we should expect some relation between the concentration and the pressure under which the fluid is excreted, but in the vine high pressures may be accompanied by a low concentration. In some cases also the fluid has almost the composition of "spring water" (Pfeffer, 1900, p. 262) which would mean a solution of very low osmotic force[1]. The marked effect of deprivation of oxygen and possibly of temperature suggests also, as in the case of *Pilobolus*, that root-pressure cannot be explained by means of simple osmotic relations but that "vital" relations of the cell involving energy transference are really involved.

The value of Pfeffer's scheme in explaining exudation and root-pressure seems to have been overlooked of late years. It has the great advantage that, although it requires a supply of energy and thus calls upon the "vital activities" of the cell it will explain the exudation of pure water from the cell. In this scheme the osmotic substance is supposed to exist in the cell at two different concentrations. It may be represented by the model in fig. 3. The curved glass tube is closed by two completely semi-permeable membranes A and B. The arm above A is filled with a strong sugar solution (say $M/1$), the arm above B with a weak sugar solution (say $M/10$), the intervening space being filled with water; the two arms are supposed to be plunged in water. On the entry of water through A and B pressure will develop in the tube and when the pressure reaches

[1] Priestley (1918, p. 199) has suggested that in "bleeding" the soluble substances which pass into the vessel below are absorbed again during their passage up the stem. The value of any theory is, however, seriously weakened when it requires the support of a subsidiary hypothesis. Furthermore if we are to fall back on the unknown processes of "physiological absorption" the theory ceases to be a physical explanation of the process. The question also arises why should the cells below give out substances and the cells above reverse the process?

that of the osmotic pressure of the solution above *B* absorption through *B* will stop, since, owing to the pressure, the solution on the one side of the membrane *B* will be in equilibrium with the water on the other side. At *A* however there will be no equilibrium at the two faces of the membrane owing to the higher concentration of the solution and water will continue to enter. As a result the pressure in the tube will go on increasing and there will no longer be equilibrium at *B*, but water will be forced out and the solution in that arm will become more concentrated. If *B* were not in water but exposed to the air water would appear at its surface. A transference of water through the tube has occurred and so work has

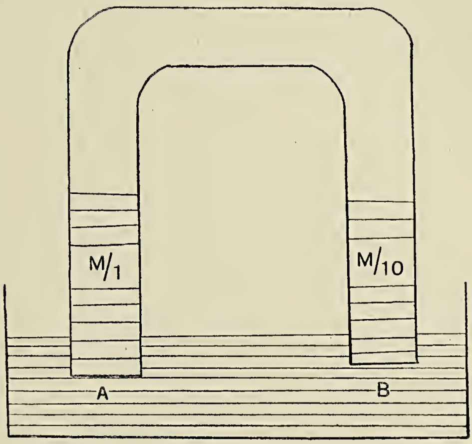

Fig. 3

been done, but there is no contravention of the second law of thermodynamics, for the process will not continue indefinitely as the two solutions will gradually mix; the work has been done at the expense of the energy of diffusion. If the process is to continue in the living cell work will have to be done to keep the two solutions at different concentration in different parts of the cell[1]. An advantage of a theory of this kind is that exudation under high pressure could be obtained, for the exudation pressure would be the difference between the osmotic pressure of the two solutions. If the membrane in contact with the solution of lower concentration is slightly permeable the

[1] Rowell (1918) following Pfeffer has a somewhat similar model but it would seem to be unworkable since the two solutions of different concentration are separated by semi-permeable membranes.

substance could diffuse out and a solution under pressure would be forced into any vessel attached at *B*.

Hitherto normal osmosis has been considered but the question naturally arises as to whether these processes of exudation can be explained by the special properties of the membrane. It is known that some membranes will bring about a "negative osmosis" in which fluid will pass from a strong solution into a weak one just as it does in the case of *Pilobolus*. There is, for example, the work of Bartell (1914) who found that porcelain membranes with pores of large size showed an increase of pressure on the side of the weak solution, while similar membranes with finer pores showed a normal pressure. Bartell and Madison (1920) have examined the effect of gold-beaters' skin used as an osmotic membrane. They found that with various solutions the normal osmotic tendency might be increased, decreased or reversed. The results can be explained by the electrical relations of the membrane; a difference of potential between the two faces of the membrane is developed if electrolytes are used and this electro-endosmosis may aid or retard the normal process of osmosis; we thus have an additional force superimposed on the ordinary osmotic relations as indicated earlier. For the production of negative osmosis energy must be available so that, as pointed out by Freundlich (1916), the phenomenon can occur if the membrane is permeable to the electrolyte as a whole, or if it is permeable to one ion only of the electrolyte, and the electrolytes on the two sides of the membrane are different and react with one another. The gold-beaters' skin membranes are leaky membranes permeable to the electrolytes as a whole so they fulfil the first condition.

The membranes of the living cell are generally more or less permeable and they are bathed with electrolytes. Differences of electrical potential can be detected in living tissue, so that the negative osmosis to be observed, through such a membrane as gold-beaters' skin, may be similar in origin to the negative osmosis which is characteristic of the exudation exhibited by the sporangiophore of *Pilobolus* and by hydathodes of the type of those on the leaf of *Phaseolus*. It is, however, doubtful if exudation under the high pressures sometimes associated with root-pressure can be explained in this way.

An attempt has been made to show that the claim of Lepeschkin that the osmotic pressure of the stronger cell contents is responsible for the exudation from the cell of a weaker solution cannot be substantiated. A number of mechanisms can, however, be suggested

by means of which this exudation could be brought about, though how far such mechanisms are actually at work in the living cell it is at present impossible to say. Much more knowledge of cell dynamics is required before we can deal satisfactorily with such difficult problems as exudation and root-pressure. Quantitative data are particularly necessary for example as to the force with which fluid can be exuded from the cell as the result of the action of electro-endosmosis or of the difference of concentration of solutions in different parts of the cell.

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REFERENCES

BAYLISS (1918). *Principles of General Physiology.* London.

BARTELL (1914). *Journ. Amer. Chem. Soc.* **36**, p. 1646.

BARTELL and MADISON (1920). Anomalous Osmose of some Solutions of Electrolytes with Gold-beaters' Skin Membranes. *Jour. Phys. Chem.* **24**, p. 444.

DELF (1916). Studies of Protoplasmic Permeability. *Annals of Botany,* **30**, p. 283.

FREUNDLICH (1916). Ueber abnorme Osmosen. *Kolloid Zeitschr.* **18**, p. 11.

HÖFLER (1920). Ein Schema für die Osmotische Leistung der Pflanzenzelle. *Ber. d. deut. bot. Ges.* **38**, p. 288.

JOST (1913). *Vorlesungen über Pflanzenphysiologie*, p. 82.

LEPESCHKIN (1906). Zur Kenntniss der Mechanismus der aktiven Wasserausscheidung der Pflanzen. *Beitr. z. bot. Centralb.* **19**, p. 409.

PFEFFER (1877). *Osmotische Untersuchungen.*

—— (1890). Zur Kenntniss der Plasmahaut u. Vakuolen. *Abh. kgl. Ges. d. Wiss.* **16**, Leipzig.

—— (1900). *Physiology of Plants*, Oxford, p. 262.

PRIESTLEY (1920). The Mechanism of Root Pressure. *New Phytologist,* **19**, p. 189.

ROWELL (1918). Zur Frage einer Reizbarkeit blutender Zelle durch hydrostatischen Druck. *Svensk Botan. Tidskr.* **12**, p. 338.

THODAY (1918). On Turgescence and the Absorption of Water by the Cells of Plants. *New Phytologist,* **17**, p. 108.

URSPRUNG u. BLUM (1916). Zur Kenntniss der Saugkraft. *Ber. d. deut. bot. Ges.* **34**, p. 525.

THE REVERSAL OF GEOTROPIC RESPONSE IN THE STEM

I. THE EFFECTS OF VARIOUS PERCENTAGES OF CARBON DIOXIDE

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(With Plate I.)

This work was undertaken with a view to obtaining further experimental evidence, bearing upon the Hydrion Differentiation Theory of Geotropism which was recently brought forward by Professor Small (*New Phytologist*, **19**, p. 49, 1920). In particular, that aspect of the theory which relates to the carbon dioxide of respiration as a differentiating factor in the growth curvatures of geotropism was in mind (*cf.* Small and Rea, *ibid.* **19**, p. 208, 1920).

According to this theory it is the hydrion concentration of the continuous phase of the protoplasm in the cells of the region of gravity perception, which determines the direction of the curvature resulting from response to the stimulus.

Under normal conditions the stem, according to this theory, is a relatively alkaline structure, because the carbon dioxide of respiration does not accumulate (most of it being used up by the plant during photosynthesis), and one result of the relative alkalinity of the continuous phase of the protoplasm in the perceptive cells is that a horizontally placed stem under normal conditions turns upwards in response to the stimulus of gravity.

If the conditions are changed so that the horizontally placed plant is growing in an atmosphere made acid by the addition of an excess of carbon dioxide, then, as a result of the accumulation of the carbon dioxide within the stem, the stem may be rendered less alkaline and the hydrion concentration of the continuous phase of the protoplasm in the perceptive cells may be raised to such a degree that the direction of the geotropic curvature will be affected. The experiments described below were carried out with the object of

discovering whether the curvature was affected under such conditions. The method of procedure in the experiments was to place the plants horizontally in an atmosphere to which known percentages of carbon dioxide had been added, and to determine the effect of such abnormal conditions on the geotropic curvature of the stem.

In the course of the work it became apparent that, with added amounts of carbon dioxide above a certain percentage, there was a very decided reversal of geotropic response, the stem structures being actually positively geotropic.

It was also equally apparent that with added quantities of carbon dioxide lower than this "certain percentage," the response to the stimulus of gravity resulted in quite a normal negatively geotropic curvature.

It therefore became necessary to determine, as closely as possible, the minimum percentage of carbon dioxide which had to be added so that there would be reversal of the normal curvature.

The different stages in the development of the work are described below.

A number of preliminary experiments were carried out in October 1920. In the first one conducted, two healthy seedlings of *Clarkia elegans*, growing in garden-soil in a box, were placed horizontally in a glass jar into which carbon dioxide was being passed at the top and from which there was an outlet at the base.

After the lapse of one day no change was noted in the seedlings, *i.e.* the stems were still quite horizontal. At the end of two days both seedlings showed a slight downward curvature of the stem and on the third day there was a very strong downward curvature.

On the fourth day the seedlings had an upward turn. This last change was probably due to the fact that, after the end of the second day, the supply of carbon dioxide was cut off from the jar, and since the jar was not darkened in any way the seedlings were able to carry on photosynthesis, thus using up the carbon dioxide from the atmosphere in the jar (which in addition was not air-tight), so that on the fourth day the atmosphere in the jar was almost back to normal. The stems of the seedlings would then become relatively alkaline again and so show the normal negatively geotropic curvature. This case of recovery may be compared with other instances to which reference will be made below.

Further preliminary experiments were carried out with seedlings of *Clarkia elegans*, *Antirrhinum* and *Helianthus*; from these experiments it became quite clear that reversal of normal curvature

resulted when carbon dioxide was present in certain quantities in the atmosphere.

It was some time before the best method of procedure was arrived at, and since these preliminary experiments were conducted on less accurate lines, they will not be referred to further in spite of the fact that the results were in accordance with the theory.

It was found, in the course of preliminary experiments, that the seedlings which gave the best results were those of *Helianthus annuus*, because they respond so readily to the stimulus of gravity under normal conditions, and because they are even more ready to show an abnormal curvature under abnormal conditions.

The following method was the one adopted in all the experiments tabulated below: A box containing sand in which were growing a number of erect, healthy seedlings of *Helianthus* was fixed in a large bell-jar so that the hypocotyls were in a horizontal position. (The bell-jars used in the experiments varied in volume from 4000 c.cs. up to 9000 c.cs.) A ground glass plate was sealed to the bottom of the jar with paraffin wax and carbon dioxide was introduced by displacement of a known volume of water, giving a percentage which was known approximately. The jar containing the seedlings was placed in a dark cupboard, in order to avoid heliotropic effects, and was examined at regular intervals. One of the properties of carbon dioxide is that it diffuses rapidly and, this being so, it may be taken that the gas in the jar was of uniform concentration throughout. Samples of gas from the top and bottom of a jar were analysed and proved to contain the same percentage of carbon dioxide. Further, as soon as a curvature in any direction was noticed, a sample of the gas in the jar was analysed. The apparatus used in the analysis of the gas in each case was a modification of the Hempel Apparatus for Gas Analysis.

The experiments carried out are tabulated below, and in each case the method adopted was exactly similar to that described above.

Date of experiment	Number of seedlings	Number of seedlings showing curvature	Volume of jar in c.c.	% CO_2 (by analysis)	Temperature ° C.
1. 1st Dec. ...	5	5 down	4000	33	14
2. 11th Feb. ...	7	7 ,,	7000	32	12
3. 11th Feb. ...	9	9 ,,	7000	29·7	12
4. 17th Jan. ...	3	3 ,,	4000	26	13
5. 19th Nov....	3	3 ,,	4000	25	14
6. 11th Feb. ...	4	4 ,,	7000	22	12
7. 25th Nov....	3	3 ,,	4000	20·9	14
8. 30th Jan. ...	2	2 ,,	9000	20	13
9. 19th Jan. ...	5	5 ,,	4000	19·6	13
10. 1st March...	5	5 ,,	7000	18	12
11. 27th Jan. ...	2	2 ,,	9000	16·8	14
12. 22nd Nov.	7	6 ,,	4000	16	14
13. 21st Jan. ...	5	5 ,,	4000	14·5	13
14. 7th Feb. ...	3	3 ,,	7000	14	11
15. 7th Feb. ...	10	9 ,,	7000	13·3	11
16. 20th Jan. ...	4	4 ,,	5500	12·6	14
17. 21st Feb. ...	2	2 ,,	7000	10·5	13
18. 18th April	7	7 ,,	7000	10·4	14
19. 1st Feb. ...	2	2 ,,	4000	10·3	13
20. 14th March	6	6 up	7000	9	14
21. 1st Feb. ...	2	2 down	4000	9	14
22. 14th March	7	7 up	7000	8·2	14
23. 25th Feb. ...	4	4 down	7000	8	14
24. 10th March	7	1 down 6 up	7000	7·9	13
25. 11th March	7	7 up	6250	7·76	15·5
26. 16th March	9	9 ,,	7000	7·6	14
27. 21st Feb. ...	2	2 down	7000	7·4	14
28. 17th Feb. ...	9	9 up	7000	7·2	14
29. 15th March	7	7 ,,	7000	7·1	14
30. 25th Feb. ...	5	5 ,,	6250	7	14
31. 25th Feb. ...	8	8 ,,	9000	6	14
32. 14th Feb. ...	2	2 ,,	7000	5·2	13
33. 15th March	9	9 ,,	7000	5·2	14

NOTES ON EXPERIMENTS

Exp. 1. The box containing the seedlings was removed from the jar on Dec. 2nd and was left horizontally in fresh air and light with the hypocotyls of the seedlings still showing the strong downward curvature. On Dec. 3rd all the seedlings showed a normal negatively geotropic curvature. This complete recovery was brought about because photosynthesis was carried on when the seedlings were in ordinary air and light, and thus the accumulated carbon dioxide was used up, the hypocotyls became again relatively alkaline and normal upward curvature resulted.

Exp. 2. All the seedlings showed normal upward curvature when left in ordinary air and light—as in the first experiment tabulated.

Exp. 3. All seedlings showed normal curvature when taken out of jar and left in air and light.

Exp. 5. Seedlings showed normal geotropic curvature after having been left in air and light for a day.

Exp. 12. These seedlings were photographed in the jar, when showing reversed curvature (see Plate I, fig. 1). The carbon dioxide was removed from the jar on the afternoon of Nov. 22nd and the seedlings left in air and light. On the following morning all the seedlings showed a normal upward curvature. They were again photographed (see Plate I, fig. 2). The hypocotyl of the 7th seedling was too short to show curvature.

Exp. 15. Nine of these seedlings showed a very definite curvature downwards at first, but after some hours two of the seedlings showed a negatively geotropic curve. The seedlings were photographed while still in the jar. An examination of Plate I, fig. 3 will show the two seedlings referred to above, and it is clear from the photograph that the first curvature was in a downward direction. The box of seedlings was taken out of the jar and after twelve hours in air and light the hypocotyls of all the seedlings showed a normal negatively geotropic curvature (see Plate I, fig. 4).

Exp. 20. These seedlings had been brought on in bright light, hence because of active photosynthesis the carbon dioxide of respiration had not accumulated to any extent before the seedlings were put into the jar. This fact would probably account for the normal curvature, because a higher percentage of carbon dioxide would be necessary to decrease alkalinity sufficiently to produce reversed curvature (see below).

Exp. 22. After four hours in the atmosphere containing 8·2 per cent. carbon dioxide, two of these seedlings showed a slight upward curvature and the remaining five were still quite horizontal. On the following morning all the seedlings had a normal upward curvature. Again in this case the seedlings had been brought on in bright light.

Exp. 23. The downward curvature was slight in these seedlings, and was not apparent until several hours had elapsed.

Exp. 24. In this experiment, response to the stimulus was much slower than the abnormal response in the higher percentages. When the six seedlings were showing normal geotropic curvature, an additional amount of carbon dioxide was passed into the jar, and the jar was replaced in darkness. After two days the hypocotyls of the seedlings (which with 7·9 per cent. carbon dioxide in the atmosphere had shown a normal curvature) had turned downwards, because the addition of the extra carbon dioxide to the jar had rendered the atmosphere sufficiently acid to raise the hydrion concentration in the perceptive cells to an extent sufficient to cause reversal of the normal curvature.

Exp. 27. These seedlings had been brought on in fairly dull light, so that there would be little photosynthesis, and therefore CO_2 would have accumulated to a certain extent. This would probably account for the reversal with the small percentage (see below).

From the results tabulated above it is quite clear that reversal of geotropic curvature actually does occur in the hypocotyls of seedlings of *Helianthus annuus*, when the seedlings are fixed horizontally in an atmosphere containing from about 9 per cent. to 30 per cent. of carbon dioxide.

With the apparatus employed in the analysis of the gas it was found that an error of 0·1 c.c. in the reading of the volume of the gas remaining after the CO_2 had been absorbed from the sample, resulted in an error of 1 per cent. either way in the percentage of carbon dioxide as analysed; when allowance is made for such an error (*i.e.* 1 per cent. in either direction) it seems reasonable to conclude from the results tabulated that the percentage of carbon dioxide necessary to produce reversal of the normal geotropic curvature in the hypocotyls of *Helianthus annuus* is approximately 7 to 10 per cent.

The minimum percentage of carbon dioxide necessary to produce such abnormal response would no doubt be slightly different even for different plants of the same species, *e.g.* in cases where the previous history of the plants used in the experiments had differed.

The factor in the previous history which would have the greatest effect would be light. If the plants were brought on in bright light then the CO_2 of respiration would be used up in photosynthesis, and, therefore, would not have accumulated to any extent in the plant. On the other hand, photosynthesis would be much less active in plants brought on in dull light. Such plants would have accumu-

lated to a certain extent the carbon dioxide of respiration, and in such a case a smaller percentage of carbon dioxide in the atmosphere would alter the alkalinity of the stem sufficiently to cause a reversal of the normal geotropic curvature. Reference is made in the "Notes on Experiments" to cases in which such previous history may have affected the direction of curvature.

In order to prove that the downward curvature of the *Helianthus* seedlings in the atmosphere containing carbon dioxide above a certain percentage really represents a reversal of geotropic curvature, experiments were carried out with a klinostat.

A box containing seven *Helianthus* seedlings was attached horizontally to a revolving klinostat. The klinostat used in these experiments had a long horizontal rod as the revolving axis, and this axis was fitted through a hole in the cork of a jar which was supported horizontally and was similar to those used in all the above experiments. The box containing the seedlings was clamped horizontally at the end of the revolving axis of the klinostat and the jar was made water-tight by means of a glass plate and paraffin wax as before. Carbon dioxide was introduced by displacement of water as before to the extent of approximately 30 per cent.

In the previous experiments in which the percentage of carbon dioxide was as high as 30 per cent. reversal of geotropic curvature was evident after a very short time ($\frac{1}{2}$ to $\frac{3}{4}$ hour), but when the seedlings were being revolved on a klinostat in an atmosphere containing 30 per cent. CO_2 there was no curvature. In this first experiment with the klinostat the seedlings were watched carefully for 6 hours, and at the end of that time they were still absolutely horizontal.

This experiment was repeated on several successive days with different sets of seedlings, with the same result, *i.e.* no curvature on the klinostat. If the downward curvature of the seedlings in the atmosphere containing above 10 per cent. of CO_2 were *not* a geotropic phenomenon, there would be curvature even when the seedlings were being revolved on the klinostat. It has been shown by these experiments with the klinostat that no curvature takes place under these circumstances, and therefore the downward curvature in all the experiments in which it occurred quite clearly represented a reversal of the normal geotropic curvature.

In conclusion, I should like to express my gratitude to Professor Small, under whose supervision this work has been carried out and whose suggestions and criticisms have been invaluable.

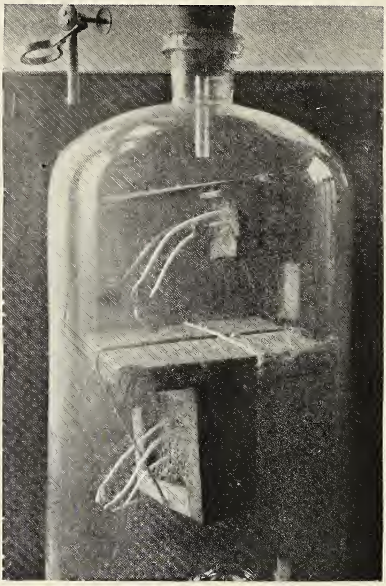

Fig. 1

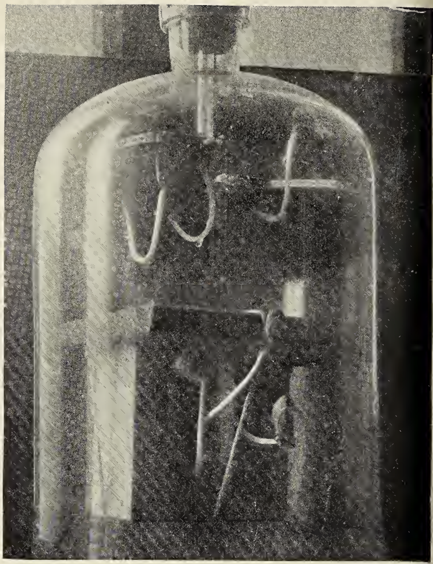

Fig. 2

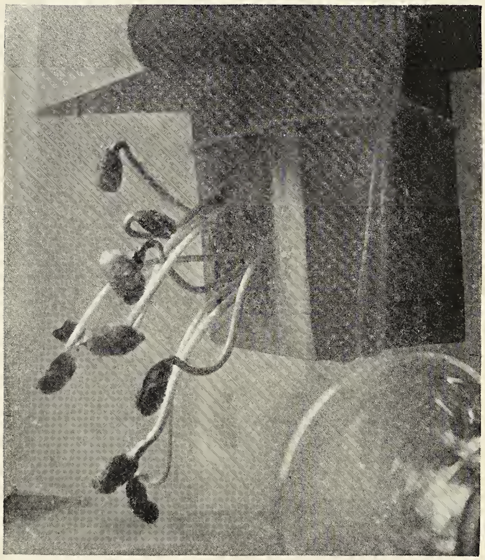

Fig. 3

Fig. 4

LYNN—EFFECT OF CARBON DIOXIDE IN REVERSAL OF GEOTROPIC RESPONSE

EXPLANATION OF PLATE I

Fig. 1. Seven sunflower seedlings, six of which show reversed geotropic curvature in 16 per cent. carbon dioxide (Exp. 12).

Fig. 2. The same about 24 hours after the excess of carbon dioxide had been removed, showing recovered normal geotropic curvature.

Fig. 3. A similar set of sunflower seedlings most of which show reversed geotropic curvature in 13·3 per cent. carbon dioxide (Exp. 15). One of the seedlings shows normal curvature, two show recovered normal response as well as a downward curvature.

Fig. 4. The same about 12 hours after they had been removed and placed in fresh air and light, showing recovered normal geotropic curvature.

REVIEWS

GENETICS AND EVOLUTION

Hagedoorn, A. L. and Hagedoorn, A. C. The Relative Value of the Processes Causing Evolution. Pp. 294. Martinus Nijhoff. The Hague, 1921. Price 9 guilders.

The authors of this very interesting book, on the basis of a long personal experience of genetic research, a wide acquaintance with the literature, and—not least important for their task—an evidently extensive knowledge of the world, of the different nations, races and classes of man, and of the breeds of domestic animals and plants, discuss afresh the still unsettled question of the factors of organic evolution. The following review does not profess to be critical. It aims simply to give the ordinary botanist some idea of what the book contains.

The authors call attention to the wide divergences of opinion still existing as to the factors of evolution, in spite of the enormous development of genetic research during the last 20 years, and to the reluctance of geneticists to make any attempt to correlate the facts so far obtained. This reluctance is not quite universal. The authors pay tribute to Bateson's subordination of the different specialised genetic investigations to the main problems of evolution[1]. "The first author," they say, "after Darwin who approached genetics in this spirit was Bateson." And Gates, in the pages of this Journal[2], and elsewhere, has recently made similar attempts. It may be urged of course that we still do not know enough of the facts to theorise safely about evolution and that we must await the results of further research before attempting to do so. It is clear in any case that general theorising about evolution must still be provisional. It can only be a question of reviewing, from time to time, the knowledge accumulated, and of endeavouring to see where we stand. This the ordinary biologist is unable to do for himself owing to the extremely specialised work of the modern geneticist, and the complicated and unfamiliar language in which it is expressed.

Meanwhile it is evident that the subject is still liable to the over-emphasis of single factors on the part of individual theorists. "There is one point common to all the theories of evolution, excepting Darwin's, and that is that each theorist has always over-emphasised one point, one single link in the chain of processes which goes to the making of species, and has brought out this point as 'the' cause of evolution. Just as Lamarck gave all his attention to adaptation [*i.e.* direct adjustment to environment] and led himself to believe that adaptation is the cause of numerous processes with which we now believe it to be

[1] *The Problems of Genetics*, Yale University Press, 1913; Presidential Address to the British Association, London, 1914.

[2] "Mutations and Evolution," *New Phytologist*, **19**, 1920. (Reprint, No. 12, 1921.)

only remotely concerned, so has Weismann over-emphasised the power of selection to the exclusion of everything else. And de Vries, who believed he had witnessed a striking instance of mutation, spontaneous origin of species, has come to believe mutation to be the sole important cause of evolution." But the modern geneticist, for the most part, takes little interest in the problems of evolution, perhaps by way of reaction from the excessive speculation and fine-drawn theorising of the post-Darwinian period at the end of last century. "No one, since Darwin," our authors consider, "has set forth a comprehensive theory of evolution worth the name."

"Every theory of evolution must account for variation, must give a plausible explanation of the causes of that variation which may be instrumental in species formation, and in the second place it must account for specific stability....Lamarck thought that the stability of a species is obtained....as soon as the species has come into a new state of equilibrium with its surroundings....Weismann thought of the final stability and purity of a species as the result of a long continued natural selection. De Vries holds that the unknown causes for the abrupt variation which produces a new species imply a new stability."

In regard to heredity the authors rightly lay stress on the great advance made by Roux when he distinguished determination factors from realisation factors. We now believe, as has been said, that "every character of an organism is both inherited and acquired." "Genetics," according to the Hagedoorns, "is essentially a branch of biomechanics, concerning itself with a study of those factors in the development of an organism which are inherited." They believe that "numerous things are transmitted from parent to offspring, each of which, by its presence in the cells, tends to influence one or more definite steps or processes in development, whenever these steps are taken or these processes undergone....no latency or semi-latency need be ascribed to these inherited things (*genes*), which in certain individuals are not factors in development and which nevertheless are transmitted by them to some of their children[1]." All inherited "factors" are genes but all the genes present in the germ are not necessarily factors in its development. The presence or absence of a certain gene may determine a definite difference in the final qualities, but it is inadmissible to speak of such a gene as the "determiner" of that quality, for all the other genes contributing to the developmental process which results in the character in question could each, and all in their turn, be called its determiner. The characters of an organism are not so many separate things, they are all the result of a great many factors, some inherited (genes), some furnished by the environment. We have every reason to believe now that every gene is present in the zygote in the same state, that every zygote is a fresh beginning, that in so far as an individual's character can be said to be determined in its germ, it is given in the combination of genes present, not in peculiar states of them.

"A vitalistic view of the nature of genes certainly fits the facts, but whereas

[1] Thus for instance there is a gene in rats, which when present in coloured animals makes otherwise black animals "agouti," but in albino rats the same gene, though it has no influence upon colour, is nevertheless transmitted in precisely the same way as in families of animals in whose development it plays an active part.

it is a theory that will work, it is not a theory one can work with." It has been shown, conclusively the authors think, that heritable variability is synonymous with genotypic impurity. In those cases where we are sure that the origin of the group ensures purity of the genotype selection has been shown to be ineffectual (Johannsen's law). Thus we do not need to make provision, in our theory of the nature of genes, for qualitative variability in the genes themselves. And this point, in their view, is the only justification for the supposition that the genes are protoplasmic. "Protoplasm is clearly an emulsion, and it must be ultimately made up of a number of non-living substances, the combination of which makes it living." The attitude of the vitalist who reasons that every constituent of protoplasm which is an integral part of it and which shows one or more of the properties of protoplasm is itself protoplasmic may be compared to the attitude "of a philosophically minded eater of plum-pudding, who should argue that the round sweet things he could dissect out of his helping, and which looked like raisins, could not *be* raisins; since he found them in his plum-pudding and forming an integral part of it they must *consist* of plum-pudding."

Quantitative propagation combined with qualitative stability is not exclusively a property of protoplasmic bodies multiplying by bipartition. Autocatalytic chemical substances fulfil both requirements, since they propagate themselves, *i.e.* suitable materials are changed into a new substance under the influence of that substance. Also they remain qualitatively unchanged[1]. The theory that genes are of this nature is believed by the authors to be compatible with all the facts known about the action of genes.

All the circumstantial evidence certainly points to the conclusion that the chromosomes are ultimately bound up with the process which leads to a distribution of the genes over cell generations, and there is no incompatibility between the view that the genes are of a relatively simple chemical nature, and that they are in some way localised in or on the chromosomes.

We may perhaps suppose that a complete set of genes is kept intact inside the nucleus, and we must probably take the view that there is no real difference between the nuclei of "germ" cells and those of "somatic" cells. The facts of regeneration of the whole plant from single somatic cells are fairly decisive for this view. But the cytoplasm of individual somatic cells of different tissues certainly has strikingly different chemical, physiological and morphological properties, and this may be due to the quantitative preponderance of one or two genes (autocatalysts) in extremely differentiated cells.

We cannot directly compare a multicellular with a unicellular organism. The cells of the former that are in immediate contact with the environment have, as a rule, no "future," *i.e.* they have no germ cells among their descendants. If we conceive of a gene as simply a chemical substance, the taking up of a new gene by a unicellular organism may not be an impossible or a rare process. But it is significant that, according to our authors, *no authentic case of a positive mutation* in the higher plants or animals is on record. And we must beware of accepting instances of the effect of selection in apparently pure clones of unicellular organisms as invalidating Johannsen's law.

[1] See A. L. Hagedoorn, *Vorträge und Aufsätze über Entwicklungsmechanik Roux.* Leipzig, 1911.

The occurrence of domestic species with new dominant characters is no argument for the occurrence of positive mutations, for such species may be the result of crossing; and even if the species crossed had not the character in question there is ample evidence that genes may be transmitted from parent to offspring through many generations without contributing to the qualities of the individuals. The hybrid between two very similar, almost identical, subspecies may have a very striking new dominant character.

The authors show that either continuous or discontinuous "variation" (in the wide sense of "difference") may be caused by a change in the genotype or by differences of environmental factors or by both acting together. So that it is impossible to suppose on the one hand, with Darwin, that only continuous variation is important in evolution, or on the other, with de Vries, that only discontinuous variation has evolutionary significance.

For the production of a character the co-operation of many genes is necessary, and the lack of any one will lead to a failure to develop a character. We cannot speak of that one which happens to be absent as the determinant of the character, any more than we can speak of one link of a chain from which a weight is suspended as holding up the weight. We can only study those genes which are in some cases absent. So long as a gene is invariably present we cannot investigate its genetic behaviour. And many genes, viz. those which are essential for the working mechanism of the organism, must be universally present. But it is possible to acquire the faculty of distinguishing differences caused by difference of genotype from those caused by environmental conditions by constantly observing, for instance, the differences between pure clones, *e.g.* nursery trees. These differences are often *made up* of apparently trivial points which might be considered as part of the fluctuating variability of the plant and attributed to differences of conditions. But the members of each clone are in fact often remarkably constant—their variability is very small. And selection between these members has no effect on the offspring. Selection is of no effect in a population without genovariability, and therefore in such a population it cannot accumulate a difference and lead to a modification of the race.

The authors take the view that dominance implies the presence of a gene which is absent in the recessive type. They counter the argument that a new dominant character must, on this view, be due to the appearance of a new gene, by referring to their contention that no gene can influence development unless there is present a given combination of other genes and non-genetic developmental factors. This is illustrated by the production of red pigment in *Primula sinensis* and a dominant yellow in mice. The case of the well-known Emily Henderson sweet peas is another instance. So that if a dominant novelty appears we cannot decide offhand that a new gene has appeared; it may be that two or more genes, none of which could produce the new dominant character unless all were present, have met and have thus produced it. They insist that we are forced in any case to look upon the production of every character as resulting from the co-operation of numerous genes, and that to consider such cases as special "complications" is a wholly mistaken view which had its origin in the fact that the first cases investigated depended on the simple presence or absence of one gene which when present completed the chain necessary for the development of a striking character.

With regard to the production of a red-fruited form in *Oenothera*, recorded by Gates, which appears to be a dominant novelty originating independently of crossing, the authors argue that since these *Oenotheras* show a remarkable suspension of combination and segregation in hybrids, characters being separately transmitted through the pollen and through the ovules, it is quite possible to suppose that in a stock originating by crossing in which this suspension had been maintained for many generations, a failure of the suspension mechanism might give rise, by the combination of genes hitherto kept separate, to a dominant novelty. In *Drosophila* also, the fly which has formed the material of so much recent genetic work, there are obviously so many irregularities in the ordinary segregation processes that it would not be surprising if Morgan's dominant novelties turned out to be produced in a somewhat similar way to that suggested for the red-fruited *Oenothera*.

Only if we are absolutely certain that the individuals of a given family are homozygous can we call the sudden production of unexpected novelties mutations in the strict de Vriesian sense. It must be noted that in America especially the term mutation is sometimes used in a much looser sense, *i.e.* as the production of *any* "novelty." The authors incline to the view that while no case of the acquisition of a new gene (positive mutation) has really been proved to occur, the loss of a gene (negative mutation) has occurred in real "pure lines" (Johannsen, Nilsson Ehle) though in animals it is well-nigh impossible to distinguish between this phenomenon and the production of a recessive novelty through rearrangement of genes.

A very important part of the authors' general theory of evolution is based on their view of the relation of heritable variability to groups of individuals (clones, families, domestic breeds, or colonies, varieties or species in nature). They use the phrase "total potential variability" for the number of genes in respect of which such a group is not pure. The potential variability of a group of organisms increases if there are taken up into the group individuals which either possess a gene or genes not present in any member of the group, or which lack genes that are the common property of all the members of the group. Potential variability differs from variability because it concerns all genes, whether they have been factors in development or not. The authors believe that the total potential variability of any group is always tending to decrease (in the absence of crossing with other groups) because the offspring of any generation are normally produced, both in nature and under domestication, from a small fraction only of the individuals of that generation; and this must lead to the dropping out from the breeding stock of part of the original total potential variability of the group. This will nearly always happen, even where the new generation is derived from a random sampling of the old, because the chances are that some combinations will be omitted, and at a greater rate of course if it is the result of a definite selection from the old. But the reduction of potential variability does not depend upon selection, it is automatic, so long as some individuals are dropped out of the breeding stock.

In the case of a self fertilised plant the reduction of variability will proceed (averaging 50 per cent. in each generation) even if all the individuals produce offspring, because Mendelian segregation will result in the daughter being heterozygous for one half the number of genes for which the mother was impure. Only in the case of a quite freely crossing group of allogamous

organisms will the potential variability of the group remain undiminished (Jennings, Pearl), but such a condition assumes indefinite increase of the group which can never in reality occur for any long period. In a word heterozygotes will produce homozygotes, but not the reverse, and thus heterozygotes will *always* tend to decrease in successive generations of a group, unless crossing is universal throughout the group and all the offspring breed. This, according to the authors, and not selection is the real explanation of the purity of species, though selection may decide the ultimate genotype for which the group will become stable. In this connexion it is interesting to note that the authors are decidedly inclined to the view that in the normal case an "adaptive" character is developed owing to causes which have no reference to its "adaptive" nature, and that selection acts by enabling the organism to occupy a new habitat as a result of the possession of the character, not by developing the character in the first instance. Botanists are becoming increasingly familiar with instances which clearly point to this mode of origin of "adaptation to environment."

It is clear that on this theory isolation of a small colony from any group will speedily result in the purity of the genotype of the colony, which will differ from the genotype of the parent group, because the total potential variability of the small colony will be very much less and will differ qualitatively from the total potential variability of the parent group, and this will happen whatever the factors bringing about isolation (geographical, physiological, or the action of the breeder). If small colonies of plants belonging to one species establish themselves on so many islands, there are at once produced so many new "species" each of which rapidly becomes pure. Adaptation may have no part at all in such a process of species differentiation, because the characters in which the new species differ from one another and from the parent species may have no survival value in any of the habitats. On the other hand if the habitats differ and there is variability in the genotype corresponding with characters which have survival value in relation to the difference of habitat, there will be a selection which will play its part in determining the genotypes of the new species.

Thus we can understand why it is that geographically isolated but clearly allied species may or may not differ in "adaptive" characters. We can also understand how it is that different closely allied species come to exist in the same geographical area but in different habitats, different "ecological niches," between which the chances of crossing are at a minimum, *without* any obvious special adaptation to their respective habitats, and in other cases *with* such obvious adaptation. Where such habitats abut on one another one often finds "intermediates" of hybrid origin.

"Isolation of some sort is necessary; without isolation even selection cannot work against the levelling effect of the factors tending to reduce the potential variability." And any kind of isolation must tend to species formation, to the production of new groups, having their own "centres of stability" (Wagner), provided there is an unequal division of total potential variability in the isolated groups. In plants which are self-fertilised or apogamous as a rule, but where crossing is not absolutely excluded, numerous species may come to exist in the same area and the same ecological niche, for the changes in genotype brought about by crossing will be stereotyped by the subsequent isolation

of different families. In such cases when crossing occurs some of the species may disappear and others originate.

Species formation is also possible in allogamous organisms inhabiting a large area where barriers are absent but the rate of dispersal is very slow (*e.g.* snails in a lake), for there the conditions in every spot will approach those of complete isolation, owing to the sedentariness of the local populations, so that a great number of local forms, the despair of the systematist, may come to exist. Very close local study will certainly distinguish a number of these local forms, while the "lumper" will include the whole series in one species. Organisms with greater powers of dispersal are much more likely to be monotypic over a wide area (*e.g.* trout in the same lake).

These considerations lead on to the question as to whether, in the light of modern genetic research, we can obtain a logical and workable definition of the term *species*. The authors define it as a group of organisms so constituted and situated that they tend, under conditions which promise to be permanent, to reduce automatically their potential variability, and this is claimed as corresponding well with the conception of the taxonomist. The usual procedure of the taxonomist, the description of a "type specimen," is certainly founded on the common experience that an enormous majority of the plants or animals grouped under the name conform to the description. The prevailing opinion among systematists is that species are realities, real groups of organisms, of which the majority are true to type, and it is unlikely that this opinion is so devoid of foundation as some modern geneticists would have us believe. If the authors are correct in their main contentions we can see that it must correspond with reality; and that it is due to the fact that in spite of crossing there is always operative in greater or less degree an automatic reduction of the variability of each group of individuals which we call a species. A variety, on the other hand, differs sufficiently from the specific type (owing to chance combination of gametes both lacking a certain gene, or supplementing one another's genotype and thus producing a new character) to demand a name, but has no permanence—it does not commonly reproduce itself as such for many generations, but is reabsorbed into the species. A variety may become a species *if it is isolated.* Thus in autogamous plants there will be no varieties. For instance Jordan's "elementary species" of *Erophila vulgaris* (*Draba verna*) are real species.

According to Darwin there is no fundamental distinction between varieties and species—varieties were for him incipient species. This is only true, according to the authors, if the condition of isolation supervenes which it generally does not. Darwin clearly showed that there is no fundamental difference between the points which distinguish species in nature and those which separate breeds of domestic animals or strains of cultivated plants. In this last contention, according to the authors, he was perfectly right. But, they add, domestic breeds *are* species. They fulfil the conditions of the definition in every respect.

In their final chapter the authors consider the status of man, and the races and nations of mankind in relation to their general view of evolution and species formation, and they are forced to conclude that the factors which keep populations or groups within a population apart have the same effect as among other animals. The logical deduction would seem to be that not only do the different nations contain separate species of man, but that all groups within a

nation which will not or do not generally intermarry are also species. The existence and relative permanence of such groups rest upon many varied grounds, but very largely on the feeling of likeness between the members of each group and the feeling of difference between their group and other groups—a likeness and difference that may depend on race, religion, occupation, mode of life, possession of land, or similar factors. To set against these differentiating factors we have the widespread desire of the bulk of the members of a nation to be alike, to be one, at least in certain respects, and even the idea of "the brotherhood of man." Mass-immigration has tended to keep the population of the United States (except the negroes and the Japanese on the Pacific coast) "one species" in spite of the great diversity of its origin, because the immigrants are, on the whole, successfully absorbed. It is probably more truly one species than the population of any other great country.

The authors rightly insist that a study of these things is essential if we are to apply the results of genetic science to political machinery, and they deprecate the exclusive attention of the eugenists to single human characters (particularly defects) of no more than varietal value at most, even when hereditary, rather than to the natural group units of the human race, which have arisen and will continue to arise as the inevitable result of universal biological and psychological processes.

The authors have scarcely taken into consideration the direct effect of environment on organisms which many botanists, in particular, hold to be one of the most important factors of evolution, though they do refer to the possibility that mutations might be induced by varying the composition of water culture solutions. This view is much more prevalent among botanists today than it was 30 years ago, when the Darwinian influence, and especially Weismann's version of Darwinism, were at the height of their power, though many botanists have always held to it. If genes are really chemical substances, it is certainly possible to believe that the long continued influence of a given environment may favour in the protoplasmic complex the production of one or several genes (for instance by dissociation or combination or by dissociation and recombination) at the expense of others. A varying "set" of metabolism may be initiated by a given environment and inherited, if only through the cytoplasm of the egg-cell; and this means the increased production of certain substances and the decreased production of others. For instance the peculiar carbohydrate metabolism of typical succulent plants (Cactaceae) leading to the accumulation of pentosans and thus to the characteristic succulent phenotype might be a case in point. But it is true that we cannot exclude the possibility that the *origin* of this type of metabolism, which has been shown to exist in plants that are not succulent in the normal habitat, may depend on a segregation of genes without any initial relation to environment. Until we have penetrated a good deal deeper into the mysteries of bio-chemistry we cannot speculate on such points with any prospect of success. Meanwhile we cannot altogether rule out the possibility of the direct effect of environment in evolution. And if it has any effect it probably has a very important effect.

A. G. T.

RECENT TEXT-BOOKS OF BOTANY

1. **Fritch, F. E. and Salisbury, E. J.** *An Introduction to the Structure and Reproduction of Plants*, 1920. Pp. viii and 458, with 2 plates and 230 figures in the text. G. Bell and Sons, London. Price 15*s*.

2. **Jones, W. Neilson, and Rayner, M. C.** *A Text-Book of Plant Biology*. Pp. viii and 262, with 6 plates and 36 figures in the text. Methuen and Co., London, 1920. Price 7*s*. 6*d*.

3. **Small, J.** *A Text-Book of Botany for Medical and Pharmaceutical Students*. Pp. x and 681, with 1350 figures in the text. J. A. Churchill, London, 1921. Price 25*s*.

Ten years ago it was still a reproach to British Botany that in spite of the existence of a few admirable elementary books (such as Scott's *Structural Botany*) students had to depend for their text-books mainly on translations from the German, though the study of modern scientific botany had long been securely established in this country. Today such a ground of reproach no longer exists. Recently we had occasion to review Professor Bower's *Botany of the Living Plant* (1919)[1], and the three works cited at the head of this review are excellent specimens, appearing within a few months of one another, of the activity of some of our middle aged and younger botanists in endeavouring to supply students with more or less comprehensive introductions to the study of plants.

In turning over the pages of these volumes one cannot but be impressed afresh with the enormous and ever-widening content of modern botany. At no time has the study of plants been more active and widespread; and it constantly tends to come into contact with more and more distinct departments of human knowledge and activity[2]. At no time, certainly, has it been of more actual and potential importance to the human race. This modern development of botany has necessarily and inevitably taken place on specialised lines, resulting in the development of numerous departments of knowledge each occupying the life-time labours of many research workers. To become thoroughly acquainted with the contents of more than a very few of these departments is quite beyond the powers of any individual.

The problem of writing an adequate introductory text-book to this vast field of knowledge is thus one of considerable difficulty. In the first place the writer has to make up his mind as to what aspects of the subject it is of the greatest importance to bring most prominently before the student. If he

[1] *New Phytologist*, **18**, p. 259.

[2] This is amusingly illustrated by the appearance on p. 191 of Professor Small's text-book, under the heading of "The Phispiral" of a reproduction of Turner's picture "Ulysses deriding Polyphemus," and on p. 394 of a diagram of the Uranium-actinium and the Uranium-radium disintegration series!

neglects this preliminary consideration he is very likely to succeed only in presenting a large number of more or less disconnected phenomena of plant life, which will tend to bewilder the mind of the reader. In an extensive work of reference such a method of treatment is perhaps justified, but in a book intended to be *read* it is fatal. In such a book the writer should set out to tell a connected story, and while the theme of this story is the same, its treatment must depend on the attitude of the writer towards plant life. From this point of view it is clear that we may have several different treatments, according as the story of plants is approached from the side, for example, of the detailed evolution of the plant world, of the physical and chemical forces at work in determining their form, structure and activities, of their relations to the actual places they occupy on the surface of the earth, or of their relations to the life of man. These aspects may of course be combined in various ways or each may serve successively as the theme of a separate section. If a choice has to be made between them we must prefer the second as the most fundamental, and after that the third and fourth. The first was dominant 20 or 30 years ago, when the tremendous stimulus to the comparative study of plant form from the standpoint of detailed evolution given by the general acceptance of the reality of the process of evolution was still fresh. Though it will always retain its interest and its vivid appeal to the imagination it must suffer from the drawback that while our knowledge of the actual causation of the variety of organic forms remains so meagre, we lack the material for a real causal treatment of the subject and tend to fall back upon teleological interpretations which are often false and always sterile.

The more fertile modes of approach are those mainly adopted in the books before us. Of these the work of Professor Fritch and Dr Salisbury must be taken in conjunction with their earlier volume, first published in 1914 and now in its fourth edition—sufficient proof of its success and popularity—*An Introduction to the Study of Plants* (Bell, 7*s.* 6*d.*). That book is an admirably clear observational and experimental introduction to botany, involving no use of the microscope and thus suitable for schools. The volume under review is intended for first year students of botany at the universities. It is divided into two parts, the first dealing with the anatomy of the seed plants and the second with the life-histories of the lower groups. The type method is abandoned, as in most of the recent books, for the sake of a more general description of the various groups, what are regarded as inessential details, which, according to the authors, have "little educational value or significance," being omitted. "Such physiology" is introduced "as is more appropriately considered in relation to microscopic structure." "Features, whether of plant-anatomy or plant-chemistry, which are of commercial importance are emphasised throughout, and it is hoped that this may serve to combat the frequent ignorance of botanical students with respect to the economic aspects of their subject." A large proportion of the illustrations are original and they are mainly taken from British or commonly cultivated plants. They are clear, well drawn and well reproduced, and demonstrate the authors' extensive first-hand acquaintance with the structural features of plants, and the careful thoroughness which they have put into the selection. The book is well written and very readable. For what it professes to be it would be difficult to improve upon, and it should be exceedingly useful to students, who will gain from its study

a clear comprehension of the nature and significance of the structural features of plants.

It would probably be a good thing to attack the question of adaptation a little more directly, even in an elementary book. The mode of exposition adopted by the authors will still, we fear, not suffice to give students clear ideas of the way in which the useful characters and powers we see in plants can originate, and the ways in which they almost certainly do not originate, though the actual statements about variation and heredity and the effect of conditions are clear, accurate and judicious enough[1]. The "teleological atmosphere" is hard to escape from altogether, but several recent American writers of elementary text-books have been very successful in freeing their statements from it, for instance Dr J. G. Coulter in his *Plant Life and Plant Uses* (1913), Dr Transeau in *Science of Plant Life* (1919)—both admirable "high school texts"—and Dr Gager in *Fundamentals of Botany* (1916), which is perhaps better known in this country. None of these authors has however attempted the direct exposition we have in mind. Something rather more constructive is wanted. Prof. Small boldly adopts the theory of epharmosis as a factor of the first importance, but the justification of this course may well be questioned.

Prof. Jones' and Dr Rayner's *Text-Book of Plant Biology* has rather a different aim. The authors point out in their preface that many students of elementary botany leave the subject before they have had an opportunity of realising its wider biological aspects, and thus miss what is often their only opportunity of acquiring that grasp of biological principles which is most desirable in the future citizen. They have therefore attempted to design an elementary course which will serve as an introduction to scientific method and enable a student to acquire an understanding of the relation of plant life to general biological knowledge.

In endeavouring to carry out these aims the authors have departed rather widely from the subject-matter of the ordinary elementary course, and though their mode of approach to the subject is exceedingly admirable in itself this fact will, we fear, tend to militate against the wide adoption of their book as a "text-book for the use of the senior classes in schools and junior classes of the University." One of the greatest obstacles to the improvement of elementary teaching is the conservatism of tradition, and the necessity under which most teachers labour of adapting their teaching to fixed examination syllabuses. We want a great deal more experiment in different methods of treatment of the subject, but it is very difficult to obtain under existing conditions. Meanwhile the multiplication of University departments in which the head is comparatively young, anxious to try new experiments in teaching, and with a nearly free hand, is all to the good.

The book under review is divided into three Parts, the first devoted to the Plant as a Machine, the second to Reproduction and the third to the Plant in Relation to the Outside World. Part I occupies nearly half the book, and contains a fairly comprehensive account of respiration, nutrition and the water relation, the treatment being essentially "biological" throughout. To each chapter there are added directions for appropriate practical work in illustration

[1] With the exception of one sentence (p. 378) which seems to imply that effective selection might take place within a pure line, though it has been stated above that this is not the case.

of the topics dealt with in the chapter. The success of one of the authors in conducting practical classes in elementary plant physiology is a guarantee of the workableness of the experiments suggested and of the practical directions given for carrying them out.

Part II contains general chapters on the process of reproduction, a very short chapter on the Outlines of Classification (the only concession to "morphology" the book contains), and another on Evolution, Variation and Heredity. This last has no directions for practical work attached. Part III consists of a chapter on Plant Response, another on Ecology and Plant Geography, and a third on the Soil.

The treatment of the subject is on the whole excellent and well calculated to fulfil the authors' primary aims. The practical drawback is that since elementary students have rarely time for more than one text-book, the omission of any treatment of morphology, which all examination syllabuses require and most teachers regard as a necessary part of the training of students, will tend to prevent the adoption of the book as a text-book in university classes.

Professor Small's book is decidedly longer, though the number of pages is considerably increased by the very numerous illustrations, and considerably more expensive than the other two. It is stated on the title-page and in the preface that it is intended primarily for medical and pharmaceutical students. The reviewer is quite clear that medical and pharmaceutical students ought not to be expected to become acquainted with so wide a range of facts and theories relating to plants as is contained in this work. It is the overloading of the syllabus in elementary biology as well as the undue preponderance of morphological detail which has been largely responsible for the desire on the part of some medical educationists to cut biology out of the syllabus altogether. This would be a deplorable action, but if it should be taken biologists will have their own unintelligent particularism largely to thank. Medical students, certainly, and probably all students who are not going to become professional botanists, should be taught not so much about plants for their own sake, but rather what plants can teach us about life as a whole. The outlook of Prof. Jones' and Dr Rayner's book is indeed much better adapted to the real educational needs of such students, though it would probably be quite impracticable to use it as a text-book in very large medical classes.

A feature of Prof. Small's book, alluded to in the preface, is the somewhat "advanced" treatment of the physico-chemical basis of physiological processes. We are inclined to agree with the author that "the average student is intelligent enough to appreciate the fundamental significance of these points, while the brighter students welcome a glimpse of what lies behind the dry bones of structural botany, and want to hear more of the inner life of the plant." At least the author's bold and straightforward method of dealing with these problems is better than the slovenly and wholly inadequate treatment which they too often receive. Another feature which will certainly be criticised is the inclusion of the author's hydrion concentration theory of geotropism, recently published in this journal, and certainly still very much "in the controversial stage." Prof. Small defends himself by saying that "in this matter these views are in the same position as many others which, in the past, have been taught dogmatically until such time as their limitations have been proved."

There is much fresh, straightforward, interesting treatment of many important topics in Prof. Small's work, but of its general plan and contents as an introduction to the subject we cannot approve. At the best it may be useful as a work of *reference* for the elementary student, but for this purpose it is hardly full enough or critical enough. We regard it as a pity that the author did not devote his remarkable gifts to the writing of a real *introduction* to botany. He has knowledge, humour, enthusiasm, courage and the power of concise yet interesting exposition, though his style, as has been said by another critic, is sometimes rather breathless. With more forethought and judgment he might, we believe, have produced the best introduction to botany that has yet been written.

The publication of these three books within a few months of one another, by heads of teaching departments, certainly does encourage the hope that the teaching of elementary botany is beginning to get into more fruitful paths.

A. G. T.

AN EXAMPLE TO BE AVOIDED.

Baines, A. E. *Germination in its Electrical Aspect.* Routledge, 1921.

Mr Baines puts down a defensive barrage in beginning the preface to his book with the following sentence:

"When this book, a plainly written account of laborious research passes into the hands of reviewers I would ask those gentlemen to remember that a great humanitarian question is involved and that while my personal opinion upon matters of detail may seem worthy of attack the fundamental truth I have put forward...is of too great importance to mankind to be passed over, or to be, to all intents and purposes, shelved by saying there is very little that is new in it." Barrages however can and must be passed through. The 'fundamental truth' which the book deals with is that the germination and growth of a plant are both governed by electrical stimuli. For example, the embryo of the dry horse chestnut seed when it falls from the tree is said to have an electrostatic charge insulated from the soil by the dry testa. When moistening occurs this charge is liberated, a current is set up and this gives the necessary stimulus to cause growth. No attempt is made by the author to examine his numerous experiments in the light of our present knowledge. In some cases the results from which he deduces evidence confirmatory of his 'truth' are explicable by well authenticated phenomena requiring no assumption of the presence of electrical currents, *e.g.* punctured acorns refused to germinate, this might be because their electrostatic charge was liberated or it might be because they had been allowed to become too dry before the experiment. In other cases the numbers of plants grown were so small that the observations are valueless, *e.g.* in one case three tufts of grass were planted out in pots and each pot was treated in a different manner. Had three thousand or even three hundred plants been taken the results might have inspired some confidence. The whole book is interlarded with the author's opinions stated without any experimental support; it also contains very numerous lengthy quotations from the works of well-known Botanists, many of which are distorted or commented on in an extraordinary fashion. In short, although this reviewer is perfectly prepared to believe in the "fundamental truth" when some sound experimental data are brought forward in its support, he has failed to find them in this book.

S. H. W.

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THE CAMBRIDGE BOTANY SCHOOL

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THE

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PERMEABILITY

By WALTER STILES

CHAPTER IV

DIFFUSION

If two gases are separated by a partition which is subsequently removed, the molecules of one gas pass into the space occupied by the other until a condition of equilibrium is reached in which the two gases are equally distributed throughout the whole space. A similar diffusion takes place in the case of two miscible liquids, except that owing to the internal friction or viscosity the rate of equilibration is much slower. Similarly, if the two liquids brought into contact consist of solutions of different substances in the same solvent, then diffusion proceeds until the solutes are equally distributed throughout the whole of the liquid; or if the solvent contains the same dissolved substance but in different concentrations in the two liquids, diffusion proceeds until the solute is equally distributed through the whole of the solvent, always supposing that no external force is operative.

Phenomena involving the diffusion of gases do indeed occur in the plant, as in the processes of carbon-assimilation, respiration and transpiration. But directly any gas reaches the surface of a cell any further passage of the molecules of the gas through the cell takes place in an aqueous medium, and in problems of permeability it is with diffusion through a liquid that we are concerned, and in most cases with diffusion through an aqueous medium.

The first systematic researches on diffusion of liquids were made by Thomas Graham (1851), who investigated the diffusion of a variety of substances dissolved in water. He showed that the quantity

of salt diffusing through unit area of the solvent depended on the concentration of the salt, on the nature of the salt, and on the temperature. The greater the difference of concentration, the more salt diffused in unit time, and the higher the temperature the faster the rate of diffusion.

The subject was later investigated by Fick (1855) who, by comparison of the problem with that of the conduction of heat worked out by Fourier, propounded the well-known equation which has come to be known as Fick's law. This equation is

$$dC = -D\frac{\partial c}{\partial x}dt,$$

where C is the quantity of salt passing through unit area in a time dt at a point x where the concentration gradient (*i.e.* the rate of change of concentration with distance) is $\frac{\partial c}{\partial x}$. The value of D is constant for any particular substance in any definite concentration and at a definite temperature and is called the coefficient of diffusion for the substance, or the diffusivity. It is thus the quantity of salt diffusing across unit area in unit time when the concentration gradient is unity (that is, when two cross-sections of the liquid at unit distance apart differ by unity in their concentrations).

Fick's law states therefore that the quantity of salt diffusing across unit area is proportional to the coefficient of diffusion, to the concentration gradient and to the time of action. This law has been abundantly verified since the time of Fick. For the solution of the differential equation reference may be made to the work of Fourier (1822, 1878) or to the various more modern works dealing with Fourier's equations (for example, Carslaw, 1906; Weber and Riemann, 1910–1912). Reference may also be made to a paper by Kelvin (1889, 1890) in which are given the curves showing the relation between concentration of solution at a point distance x from the initial surface of contact between water and a saturated solution, the position of the point x, and the time of action.

It will be sufficient here to consider only the simplest case, that of a salt diffusing into a cylindrical column of water. If we regard the column of water as infinitely long, the solution of Fourier's equation for this case is

$$u = u_0\left\{1 - \frac{2}{\sqrt{\pi}}\int_0^q e^{-q^2}\,dq\right\},$$

where $$q = \frac{x}{2\sqrt{Dt}},$$

and u is the concentration at a point in the cylinder distant x from the initial surface of contact between water and the solution, and after a time t has elapsed from the commencement of diffusion, u_0 is the concentration of the original solution at the mouth of the cylinder and D is the coefficient of diffusion. The value of

$$\frac{2}{\sqrt{\pi}}\int_0^q e^{-q^2}\,dq$$

for different values of q is given in tables of the probability integral (see, for example, Peirce, 1910).

It follows from this equation that if u is constant, that is, if we consider the march forward into the column of water of a particular concentration of diffusing substance, that q must also be constant. Hence

$$\frac{x}{2\sqrt{Dt}} = \text{constant},$$

or, stated in words, the distance any particular concentration of salt has reached is proportional to the square root of the time of action and to the square root of the coefficient of diffusion. This relation has been repeatedly verified (Coleman, 1887, 1888; Chabry, 1888; Voigtländer, 1889).

Various methods have been devised for the measurement of coefficients of diffusion. These may be classified as follows:

(1) Those depending on the estimation after a certain time by chemical analysis of the concentration of the solution occupying different layers in the vessel in which diffusion is proceeding.

(2) Methods in which the concentration of different layers of solution is determined from estimations of the density of the solution.

(3) Methods based on the estimation of the rate at which substances go into solution.

(4) Indicator methods in which the presence of an indicator in the liquid shows when a certain concentration of the diffusing substance is reached at any particular place.

(5) Electrical, and (6) optical methods.

For a description of these various methods reference may be made to the article on Diffusion by Waitz (1908) in Winkelmann's *Handbuch der Physik*. An electrical conductivity method is described by Haskell (1908).

In Table IV are given the coefficients of diffusion of a number of substances in water. These values are taken from the results of Thovert (1901, 1902), Scheffer (1888), Schuhmeister (1879) and Heimbrodt (1903, 1904), and the calculations made by Stefan (1879) from the data of T. Graham.

TABLE IV

Coefficients of Diffusion of Various Substances

Substance	Concentration in gm.-mols. per litre	Tempera-ture in °C.	Coefficient of Diffusion in $\frac{cm.^2}{sec.} \times 10^{-5}$	Observer
HCl	3·2	19·2	4·50	Thovert
,,	0·02	19·2	2·45	,,
HNO_3	3·9	19·5	2·85	,,
,,	0·02	19·5	2·45	,,
H_2SO_4	2·85	18·0	1·85	,,
,,	0·005	18·0	1·51	,,
KOH	3·9	13·5	2·81	,,
,,	0·02	13·5	1·95	,,
NaOH	3·9	12·0	1·14	,,
,,	0·02	12·0	1·30	,,
KNO_3	3·9	17·6	1·03	,,
,,	0·02	17·6	1·48	,,
KCl	2·95	17·5	1·85	,,
,,	0·02	17·5	1·57	,,
NaCl	3·9	15·0	1·18	,,
,,	0·02	15·0	1·09	,,
$CaCl_2$	1·22	9·0	0·83	Scheffer
,,	0·0468	9·0	0·79	,,
K_2SO_4	1·5	10	0·87	Schuhmeister
,,	0·95	19·6	0·92	Thovert
$ZnSO_4$	2·95	19·5	0·38	,,
,,	0·025	19·5	0·58	,,
$MgSO_4$	3·23	10	0·31	Scheffer
Ethyl alcohol	3·75	11	0·52	Thovert
,, ,,	0·05	11	0·85	,,
Glycerin	1·75	10·14	0·35	Heimbrodt
,,	0·125	10·14	0·41	,,
Citric acid	0·0303	4·5	0·39	Scheffer
Sucrose	1·97	18·5	0·15	Thovert
,,	0·97	18·5	0·28	,,
Albumin	—	13	0·073	Graham-Stefan

From the numbers given in this table it will be observed that the coefficient of diffusion varies considerably for different substances. It is also dependent upon the concentration of the diffusing substance, upon the temperature and upon the nature of the medium through which diffusion is taking place. In the following discussion, except where expressly stated otherwise, the medium is always assumed to be water.

As regards the influence of the nature of the substance on the coefficient of diffusion, generally speaking the diffusivity is high for electrolytes and substances of low molecular weight, while it decreases with increasing complexity of the molecule, being lower for substances like sugars and very low for colloidal substances. Of the commoner electrolytes, acids and alkalies diffuse most rapidly, and

in general electrolytes with the highest diffusivity have the highest electrical conductivity.

Mathematical formulae have been evolved to express these relations in the case of diffusion of non-electrolytes. Thus Sutherland (1905) and Einstein (1905, 1906) derived the formula

$$D = \frac{RT}{N} \cdot \frac{1}{6\pi\eta\rho},$$

where D is the coefficient of diffusion, R is the gas constant, T the absolute temperature, N the Avogadro constant (that is, the number of molecules in one gram molecule), η the viscosity of the solvent, and ρ the radius of the diffusing molecules which are assumed large in comparison with those of the solvent. Sutherland showed, however, that should the molecules of the solvent be large in comparison with those of the solute, the relation more nearly approximates to

$$D = \frac{RT}{N} \cdot \frac{1}{4\pi\eta\rho}.$$

Von Smolukowski (1906) obtained a similar expression but with a different constant, his formula being

$$D = \frac{64}{27} \cdot \frac{RT}{N} \cdot \frac{1}{6\pi\eta\rho}.$$

A general confirmation of this formula experimentally has been made by Svedberg and Andreen-Svedberg (1909, 1911) who could not, however, decide whether the constant in the equation of Einstein, Sutherland and von Smolukowski is 1 or 64/27.

The relation between molecular size and coefficient of diffusion has been stated in another form by Exner (1867, 1874, 1877) for the case of gases. Exner's conclusion is expressed by the equation

$$D\sqrt{M} = k,$$

where D is the coefficient of diffusion, M the molecular weight and k a constant. This relation has been extended to the case of non-electrolytes by Öholm (1910), who confirmed it experimentally for a number of sugars and other substances, and who used it to determine the molecular weight of dextrin from the coefficient of diffusion of the latter. A third formula has been proposed by Herzog (1910), namely

$$D\eta \sqrt[3]{Mv} = \text{constant},$$

where v is the specific volume and the other symbols have the signification already assigned to them. This relation is stated to hold for a number of non-electrolytes (Padoa and Corsini, 1915).

There seems thus good reason for concluding that the coefficient of diffusion is related in inverse fashion to the complexity and magnitude of the molecule.

With regard to the connection between coefficient of diffusion and electrical conductivity, Nernst (1888) put forward the following equation to express the relation between diffusivity and ionic mobilities:

$$D = RT.\frac{uv}{u+v},$$

where u and v are the ionic mobilities of anion and kation, and the other symbols have the same signification as before. Nernst himself realised that this formula could only be approximately correct as the diffusivity varies with concentration, nor does the formula take into account the diffusion of the undissociated part of the molecule.

To allow for the influence of concentration on diffusion, Wiederburg (1899) modified Nernst's formula as follows:

$$D_c = RT\left(\frac{2uv}{u+v} - w\right)\left(1 + \frac{4C}{K}\right)^{-\frac{1}{2}} + w,$$

where D is the coefficient of diffusion at a concentration c, K the dissociation concentration at the concentration and temperature in question, and w the molecular mobility.

Arrhenius (1892) obtained good agreement between experiment and the equation

$$D_c = D_\infty\left(1 + \frac{2BC}{RT}\right)\left(1 - \frac{\alpha C}{2}\right)^2,$$

where D_∞ is the coefficient of diffusion at infinite dilution, α a constant depending on the viscosity, and B a constant.

Arrhenius found the coefficient of diffusion of hydrochloric acid and of potassium hydroxide increased with increasing concentration, but that the reverse was the case with acetic acid, sodium hydroxide and sucrose. Scheffer also found an increase of diffusivity with increasing concentration in the case of hydrochloric acid; with sodium and potassium chlorides he found no notable change, while with sodium nitrate, sodium thiosulphate and silver nitrate the diffusivity diminishes with increasing concentration. A careful investigation of the influence of concentration on diffusivity of a number of electrolytes has been made by Öholm (1905); the data in Table V are taken from among his results. Data with regard to the influence of concentration on diffusion of glycerin, urea, sodium chloride and hydrochloric acid are given by Heimbrodt (1903, 1904).

TABLE V

Influence of Concentration on the Diffusivity at 18° C.
(Data from Öholm)

Concentration in gram-equivalents per litre	Coefficient of Diffusion in $\frac{cm.^2}{sec.} \times 10^{-5}$			
	NaCl	KCl	HCl	KOH
0·01	1·35	1·69	2·69	2·20
0·02	1·33	1·66	2·64	2·19
0·05	1·32	1·63	2·61	2·17
0·10	1·29	1·61	2·58	2·15
0·20	1·27	1·58	2·55	2·13
1·00	1·24	1·54	2·57	2·15
2·00	—	1·53	—	2·19
2·8	1·23	—	—	—
3·6	—	1·55	—	—
5·5	1·23	—	—	—

That the rate of diffusion of substances increases with rise of temperature was observed by Graham. Since these early observations quantitative determinations on the effect of temperature on the diffusivity have been made for a number of substances. Weber (1879) found that for every rise in temperature of 1° C. the coefficient of diffusion of zinc sulphate in water increased by about 0·026 of its value at 18° C. Later Seitz (1898) confirmed this value and obtained a similar one (0·024) for zinc acetate. A number of substances were examined by de Heen (1884) at temperatures varying from 15° to 60° C. In Table VI are shown the values he obtained for the coefficient of diffusion at any temperature θ, this being measured in centigrade degrees distant from 60° C. taken as zero, and reckoned as positive *downwards* from 60° C.

TABLE VI

Influence of Temperature on the Coefficient of Diffusion
(Data from de Heen)

Substance	Coefficient of Diffusion in $\frac{cm.^2}{sec.} \times 10^{-5}$
$MgSO_4$	$0{\cdot}85\ (1 - 0{\cdot}0119\,\theta)$
KNO_3	$3{\cdot}07\ (1 - 0{\cdot}0127\,\theta)$
NaCl	$2{\cdot}72\ (1 - 0{\cdot}0121\,\theta)$
Na_2HPO_4	$2{\cdot}06\ (1 - 0{\cdot}0128\,\theta)$
K_2CO_3	$1{\cdot}63\ (1 - 0{\cdot}0127\,\theta)$

It will be noticed that the relative increase in diffusion for the same rise in temperature is almost independent of the substance

among those examined, although the absolute coefficient of diffusion varies greatly. These results agree well with those obtained for zinc salts to which reference has already been made.

On theoretical grounds Nernst (1888) propounded the formula

$$D_\theta = D_{18}\,[1 + \alpha\,(\theta - 18)]$$

to express the influence of temperature on the coefficient of diffusion, D_θ and D_{18} being the coefficients of diffusion at $\theta°$ C. and 18° C. respectively, and α a constant having the value 0·026 for neutral salts and 0·024 for acids.

Assuming the correctness of Nernst's general formula, the value of the temperature coefficient α in Nernst's equation has been calculated by Öholm from measurements of the coefficient of diffusion of a number of electrolytes (Öholm, 1902, 1905) and non-electrolytes (Öholm, 1910) at temperatures between 0° and 20° C. The values found by him are summarised in Table VII.

TABLE VII

Temperature Coefficient of Diffusivity of a number of substances (Data from Öholm)

Substance	Temperature Coefficient
HCl	0·019
NaCl	0·025
KCl	0·0235
LiCl	0·027
KI	0·0235
NaOH	0·023
KOH	0·021
Acetic acid	0·028
Sucrose	0·032
Lactose	0·032
Maltose	0·032
Raffinose	0·032
Arabinose	0·044
Dextrin	0·035
Nicotine	0·016

Although there are obvious exceptions, Öholm concludes that in general the temperature coefficient of diffusivity is less the greater the diffusivity. Thus hydrochloric acid, with its very high coefficient of diffusion, has a very low temperature coefficient of diffusivity, while the slow diffusing sugars have temperature coefficients considerably higher than those of neutral inorganic salts.

It should be noted that it is assumed by all workers that the relation between diffusivity and temperature is a linear one. While this may be approximately true over the small temperature intervals with which Öholm worked, it is scarcely likely to be an exact

representation of the facts over a wide temperature interval; it may be sufficiently accurate over the temperature range with which we are generally concerned in living organisms.

We have so far considered the laws of diffusion in a medium which at equilibrium is homogeneous. In the organism, as we have seen, we have to deal very largely with heterogeneous systems. As the simplest case of a heterogeneous system we may consider two immiscible liquids separated by a phase boundary. That such systems actually occur in the living cell there can be little doubt. If a solute is soluble in both the liquids, its distribution when diffusion has proceeded to equilibrium will not be uniform throughout the system; on the contrary, the solute generally distributes itself unequally between the two solvents. This phenomenon was investigated by Berthelot and Jungfleisch (1869–1872) and later by Nernst (1891). It is found that if a substance has the same molecular complexity in the two solvents the ratio of the concentration of the solute in one solvent to its concentration in the other is a constant whatever the concentration. Thus if c_1 is the concentration in one solvent and c_2 the concentration in the other solvent,

$$\frac{c_1}{c_2} = K,$$

where K is a constant and called the *partition coefficient* or the *distribution ratio*. If several solutes are present together each one distributes itself between the solvents according to its own partition coefficient independently of the others; that is, K is independent of the presence of other solutes.

If the solute should undergo polymerisation in one of the solvents, the partition law becomes modified to

$$\frac{c_1}{c_2^{1/n}} = K,$$

where n represents the number of molecules associated together in one of the solvents.

With the law of partition coefficients may be compared the law governing the distribution of a substance between a solvent and an adsorbent at equilibrium. The quantity $\frac{x}{m}$ in the adsorption equation is of the nature of a concentration, and if for this we write c_1, and if for the concentration of the solute at equilibrium we write c_2, the adsorption equation becomes

$$\frac{c_1}{c_2^{1/p}} = K,$$

which represents the distribution of the solute between solvent and adsorbent. The similarity of this equation to that of the partition law is obvious.

The principle involved in the partition law has been applied with great success to the separation of substances which otherwise have so far been found inseparable, or are only separable with great difficulty. The separation of the four pigments of the green leaf by Willstätter (1913) is almost entirely based on the different partition coefficients of the four pigments and the substances with them, in the commoner organic solvents.

It is now necessary to consider how far the laws governing the rate of diffusion are modified in more complex systems.

The case of an electrolyte diffusing in a solution of another substance instead of in pure water has been investigated by Öholm (1912). He found that the presence of a non-electrolyte such as glycerin or sugar appreciably reduces the rate of diffusion. In the following table are given the values obtained by Öholm for the coefficients of diffusion of potassium chloride in solutions of non-electrolytes of different concentrations.

TABLE VIII

Diffusion of Potassium Chloride in Solutions of Sucrose and Glycerin of Various Concentrations
(Data from Öholm)

Substance	Concentration in gram-mols. per litre	Coefficient of Diffusion at 18° C. in $\frac{\text{cms.}^2}{\text{sec.}} \times 10^{-5}$
Sucrose	0·0	1·535
,,	1·5	0·486
,,	2·0	0·255
Glycerin	5·0	0·501
,,	7·48	0·201

We now come to the important question of the diffusion of substances in colloidal systems. The diffusion of various substances in gels has received a considerable amount of attention, partly because of its obvious bearing on physiological problems (cf. Chapter II), and also because it lends itself more readily in some ways to investigation than diffusion in free liquids.

It was concluded by Graham (1861) that sodium chloride diffused as rapidly through gelatine as through water. De Vries (1884) on the other hand concluded from observations of the colour that

potassium chromate diffuses more slowly through 4 per cent. gelatine than through water, and Coleman (1888), examining the diffusion of a number of electrolytes in gels, also concluded that the presence of the jelly brings about a retardation in the rate of diffusion. Hagenbach (1898) came to a similar conclusion in regard to the diffusion of gases in gelatine. Henri and Calugareanu (1903), from observations on the diffusion of a number of dyes in water and 1, 3 and 5 per cent. gelatine, concluded that the rate of diffusion was the same through the gelatine as through water if the former had not set to a gel, but that if this had taken place, the rate of diffusion was slower. Bechhold and Ziegler (1906) concluded that electrolytes and non-electrolytes diffuse through gelatine and agar gels more slowly than through water.

Öholm (1913) compared the diffusion of potassium chloride from a normal solution into gels of 2, 5 and 10 per cent. gelatine. His results, summarised in the accompanying table, indicate very clearly the retarding effect on diffusion of the gelatine.

TABLE IX

Diffusion of Potassium Chloride from a Normal Solution into Gels of Gelatine of Various Concentrations (Data from Öholm)

Concentration of Gelatine in per cent.	Kind of Gelatine	Coefficient of Diffusion at 20° C. in $\frac{cm.^2}{sec.} \times 10^{-5}$
2	Kahlbaum (golddruck)	1·52
5	,, ,,	1·44
10	,, ,,	1·31
2	A brand from Dundee	1·50
5	,, ,, ,,	1·41
10	,, ,, ,,	1·28

If these numbers are compared with those given in the preceding table it will be observed that, as Öholm points out, a gelatinous body affects the diffusion of an electrolyte in just the same way as any other non-electrolyte. Unpublished observations of Stiles and Adair indicate that the presence of gelatine decreases the rate of diffusion of sodium chloride progressively with increase in concentration of the gelatine. There can be no doubt that the coefficient of diffusion of electrolytes is less in gels of gelatine than in water.

Voigtländer (1889) made a study of diffusion in agar-agar gels varying in concentration from 1 to 5 per cent. and found that the

rate of diffusion was practically independent of the concentration of the gel. Sodium chloride, magnesium chloride and hydrogen chloride were among the substances examined, but the unpublished researches of Stiles and Adair have failed to confirm this conclusion in the case of sodium chloride, which appears to diffuse more slowly the greater the concentration of agar-agar, so that agar-agar behaves in the same way as gelatine in reducing the rate of diffusion.

The consequence of Fick's law in the case of linear diffusion in one direction, namely that $x = C\sqrt{Dt}$ where C is a constant (see p. 139), has been confirmed for diffusion into gels by Coleman (1888), Chabry (1888), Voigtländer (1889), von Fürth and Bubanović (1918), Stiles (1920) and Adair (1920), these various authors using a great variety of diffusing substances and gels of gelatine, gelose and agar-agar. The law holds equally well when the gel contains an indicator to mark the progress of a layer of definite concentration provided the concentration of the indicator does not approach too near to that of the diffusing substance (Stiles, 1920).

There are few observations on the influence of temperature on the coefficient of diffusion in gels. The results of Voigtländer on diffusion in agar-agar gels indicate a greater increase in diffusivity brought about by an increase in temperature from 20° C. to 40° C. than that brought about by an increase from 0° C. to 20° C. Voigtländer employs the equation

$$D_\theta = D_0 (1 + \beta\theta)^2$$

to express the relation between the coefficient of diffusion and temperature, D_θ and D_0 being the coefficients of diffusion at θ° C. and 0° C., and β a constant. It will be observed that as the values of β are small (0·01 to 0·02) in comparison with unity, when θ is also small then approximately

$$D_\theta = D_0 (1 + 2\beta\theta),$$

since the term $\beta^2\theta^2$ is small in comparison with $1 + 2\beta\theta$. Consequently, when θ is small the relation between the temperature and the coefficient of diffusion is approximately a linear one as assumed by de Heen, and by Öholm following Nernst. But when θ is large the term $\beta^2\theta^2$ is not negligible, and the coefficient of diffusion increases more rapidly with rise in temperature the higher the temperature. The unpublished results of Stiles and Adair on the diffusion of sodium chloride in agar-agar gels at temperatures from 0° C. to 40° C. support this latter assumption rather than the opinion of a linear temperature coefficient.

The observations of Chabry (1888) show that the course of diffusion of an electrolyte through a dead animal tissue is similar to its diffusion through a gel. Prismatic pieces of hyaline cartilage stained with orcein were fitted into a tube and any space between the tissue and the tube were filled with a transparent oil. The penetration of acid into the tissue was then followed by the indicator method in the same way as in the case of a gel, and it was found that the consequence of Fick's law, that $\frac{x}{\sqrt{t}}$ = constant, held in this case as well as in the cases of diffusion in water and in gels. The value of the constant was however found to be considerably less than with diffusion into a gel.

The diffusion of crystalloids through colloidal systems such as gels and dead organic tissue apparently proceeds in the same way as through water, although less rapidly. But the diffusion of colloids differs strikingly in a simple liquid and in a colloidal system. It is well known that Graham drew the fundamental distinction between colloids and crystalloids on account of the non-diffusibility of the former through membranes of parchment and other colloidal materials, while crystalloids diffused readily through such membranes. The diffusibility or non-diffusibility of a substance or group of substances through membranes is however generally not an absolute property of the membrane; it is a matter of degree. Thus colloidal membranes which are permeable to crystalloids do not let them all through equally readily. This is a matter of obviously great importance in relation to permeability of living tissue and requires to be considered in some detail; it therefore forms the subject of the next chapter.

(*To be continued.*)

A STUDY OF SOME OF THE FACTORS CONTROLLING THE PERIODICITY OF FRESHWATER ALGÆ IN NATURE

By WILLIAM J. HODGETTS, M.Sc.

(With 11 figures in the text)

I. INTRODUCTION

This paper deals with the periodical phenomena of the algal vegetation of a small freshwater pond. The research was undertaken not only for the purpose of elucidating the periodicity of the chief algal species present, but also with the object of demonstrating what dependence, if any, exists between the development and reproduction of the various Algæ, and the meteorological and other conditions, special attention being paid to the part played by the concentration of the water. Throughout the paper the principle of limiting factors[1] has been employed in discussing the influence of these various external conditions upon the growth and reproduction of the Algæ of the pond. The pond chosen is situated near Hawkesley Hall (and thus in the sequel is termed Hawkesley Hall Pond), $1\frac{1}{2}$ miles from King's Norton, near Birmingham, and the observations extend over a period of $3\frac{1}{2}$ years, namely from January 1918 to June 1921, and are based upon numerous samples collected at monthly (at times fortnightly) intervals.

The pioneer work on algal periodicity, as observed in small ponds, was commenced in this country by F. E. Fritsch (13, 14), and later Fritsch and Rich published a series of "Studies on the Occurrence and Reproduction of British Freshwater Algae in Nature" (16, 17, 18). Many of the conclusions arrived at by these workers have been confirmed by the present writer in the observations recorded below. Other contributors to the study of algal ecology in this country are G. S. West (31), and also W. and G. S. West (32, 33, 34), although the papers quoted of the latter authors deal mainly with the periodicity of the phytoplankton of British lakes. The comparatively recent account of the occurrence of freshwater Algæ in nature by the late Prof. G. S. West (31, pp. 418-451) is a useful though necessarily short *résumé* of our knowledge of the subject up to 1916.

B. M. Griffiths (19) has studied the algal conditions of a pool near

[1] A principle first utilized in algal ecology by Fritsch and Rich (16, 17, 18).

Kidderminster, and E. M. Delf (12) has given an account of the algal periodicity observed in ponds on Hampstead Heath; while continental workers on the periodicity of freshwater Algæ are Comère (6, 7, 8), Rabanus (26), and also Pevalek (24). Reference will not be made to all the workers who have investigated experimentally the relation between the growth of Algæ and various cultural conditions, as many of these artificial conditions are never realised in nature—although, as pointed out by Fritsch (14), they may be paralleled.

The chief American worker on the subject is E. N. Transeau (27, 28), who has published results based on 7½ years continuous records of the algal conditions in Central Illinois; while other American contributors are H. B. Brown (4), Copeland (9), Platt (25), and more recently Andersen and Walker (1). Various workers in America have investigated the relation between algal growth and the dissolved gases of the water, and in this connection reference may be made to the interesting papers of Birge and Juday (3), and Chambers (5), further literature being cited by these authors.

It has not been thought necessary in a paper of this sort to refer to all the numerous workers who have contributed to our knowledge of the freshwater phytoplankton, since this constitutes rather a special branch of algal biology, requiring methods of attack somewhat different from those adopted in the present line of research; but papers on the freshwater plankton are occasionally referred to in what follows. As pointed out by Fritsch and Rich (18), and West (30), the smaller pieces of water are alone suitable for demonstrating the relations between external conditions and algal growth, since larger bodies of water react much more slowly to variations in the meteorological and other conditions than do ponds and small bodies of water generally.

II. GENERAL ACCOUNT OF HAWKESLEY HALL POND AND ITS PHANEROGAMIC FLORA

Hawkesley Hall Pond is situated in a meadow about ¼ mile N.W. of Hawkesley Hall, and is not at all large, its area, when the height of the water is at a maximum, being roughly 300 sq. metres, while the greatest depth, although not known exactly, is probably between 1½ and 2 metres. It is an irregular triangle in shape (cf. Fig. 1), with the marginal banks for the most part rather low, and almost all round the pond bearing a thick growth of rushes, together with other Phanerogams (see below). There are no trees at the margin of the pond, the nearest being a few oaks by the fence (shown in Fig. 1)

on the west side of the pond. These trees, however, could cast only a feeble shade over the extreme west side of the pond during the evenings[1]. The pond is thus in a very exposed, unshaded locality,

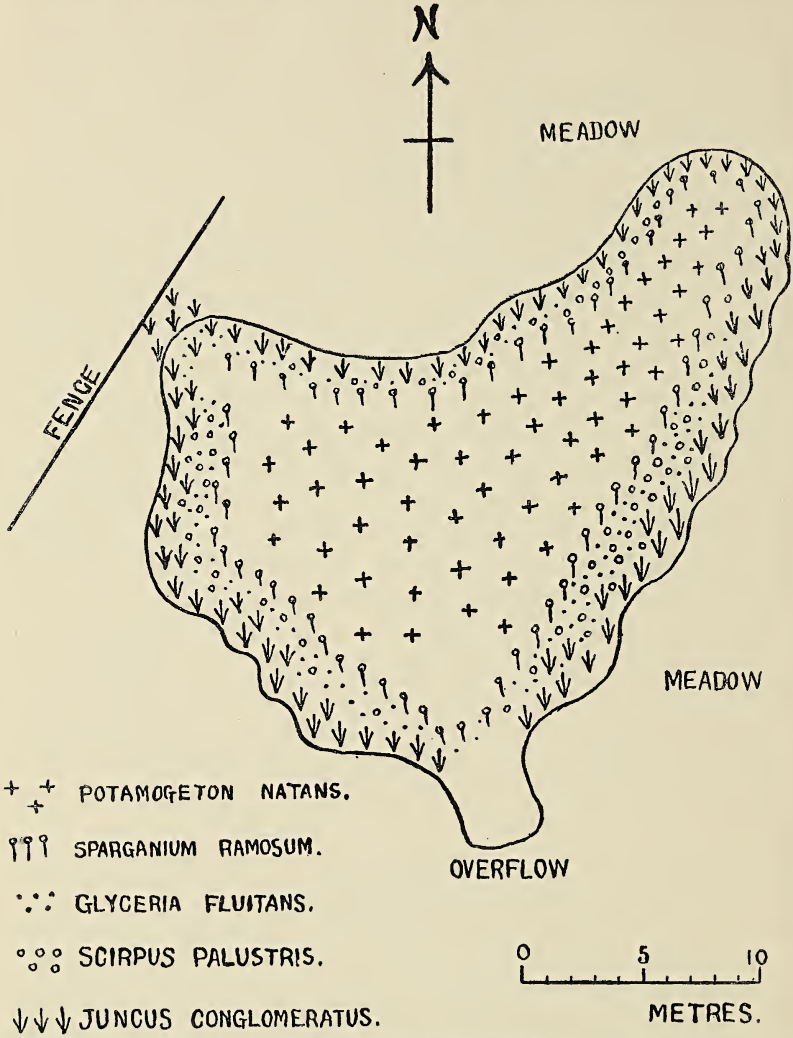

Fig. 1. Rough sketch-map of Hawkesley Hall Pond, showing the distribution of the Phanerogamic Vegetation in July 1920.

receiving practically the full force of the sun and wind, and consequently is rapidly affected by the varying meteorological conditions.

[1] A few low hawthorn bushes are present on the N.W. side of the pond, but they do not cast any shade over the pond.

On the extreme west side of the pond is a patch of marshy ground, passing under the fence, and by means of which the pond, during times of very high water, is put in temporary communication with another smaller pond (not shown in Fig. 1) located on the opposite side of the fence. This second pond is very much shaded by trees, and has not proved very suitable for a study of algal periodicity; in the present paper it is not again referred to.

The soil of the district overlies Keuper Marl, and round the pond is of the nature of a rather marly clay, which is very impervious when wet. The general surface of the meadow slopes upwards towards the pond, which is situated at the highest point of this particular field, but towards the north-west the ground rises gently again, and it is mainly water which drains off the land from this direction which feeds the pond. Since the latter never completely dries up even during the hottest weather—although at such times it contracts in volume considerably—it seems likely that there may be a bottom-spring which to a certain extent supplies the pond, but this point was not definitely settled. When flooded with heavy rain the water overflows at the shallow south corner, and drains off down the sloping meadow, so that it is impossible for the water-level to exceed a certain maximum height, which is determined of course by the height of the ground at the southern overflow corner. The pond is some distance from a road, and no field-path runs near it, and on the whole it is allowed to remain comparatively undisturbed, which to some extent may account for the richness of its algal flora.

During the summer months the pond supports an abundant phanerogamic flora, which exhibits a more or less zonal arrangement round the pond (Fig. 1). Four well-marked zones can be recognised generally throughout the summer, these being, commencing with the outermost:

(1) a zone of *Juncus conglomeratus*;
(2) a zone of *Scirpus palustris* and *Glyceria fluitans* (these species generally co-dominant);
(3) a zone of *Sparganium ramosum*; and
(4) a central area of *Potamogeton natans*.

The marginal zone of rushes is well-marked and extends all round the pond, with the exception of the south overflow corner, covering the damp banks just above water-level. *Juncus conglomeratus* being a markedly social spécies it is generally easily able to exclude competitors, but a few marsh-loving plants (*e.g. Galium palustre*) are sometimes present.

The second zone of *Scirpus palustris* and *Glyceria fluitans* is rather a mixed one, but for the most part these two species are co-dominant, although in places *Scirpus palustris* alone is dominant. *Alisma Plantago* occurs sporadically. This zone is absent altogether in places, while it rarely extends into water deeper than 20 cm.

The third zone (of *Sparganium*) is very well-marked and extends practically all round the pond (see Fig. 1), and varies in width from 45 to 120 cm.—the latter where the slope of the bottom is very gradual, as on the east side of the pond.

All the central region of the pond is occupied by the *Potamogeton natans*—a plant which has an important influence upon the algal vegetation of the pond, as will be seen later. During the winter and early spring (November to March) the *Potamogeton* is dormant, but development commences usually in early April, and by the end of June, or in early July, a great part of the water-surface of the pond is covered by the floating leaves of this plant, the spaces between the leaves being generally occupied by floating masses of filamentous Algæ. It flowers in June and July. In September its leaves gradually decay, while by the end of October all the leaves are dead, many being free and decaying in the water.

The pond is very similar in its phanerogamic vegetation to those described by Walker (29), at Bramhope, near Leeds, all the zones of vegetation (except the second) occurring in Hawkesley Hall Pond being represented in the Bramhope ponds. Doubtless ponds of this type, with similar or nearly similar phanerogamic plants, are frequent in many parts of the country; they are certainly not uncommon in the midland counties.

III. METEOROLOGICAL DATA

The more important meteorological data for the purpose of this study are those of temperature, rainfall, and bright sunshine. At the time of collecting the monthly samples of Algæ the temperature of the water and of the air near the pond were recorded, but these are not given here, since they have been found to emphasise rather too much merely temporary and often very fleeting temperature-conditions which by chance obtained at the time the samples were being collected. Of the three temperature-curves given in the lower part of Fig. 2 the uppermost gives the average maximum temperature of the air, and the lowest the average minimum for each month, while the middle curve gives the mean of these two; the data being taken from the official Monthly Weather Reports (Birmingham

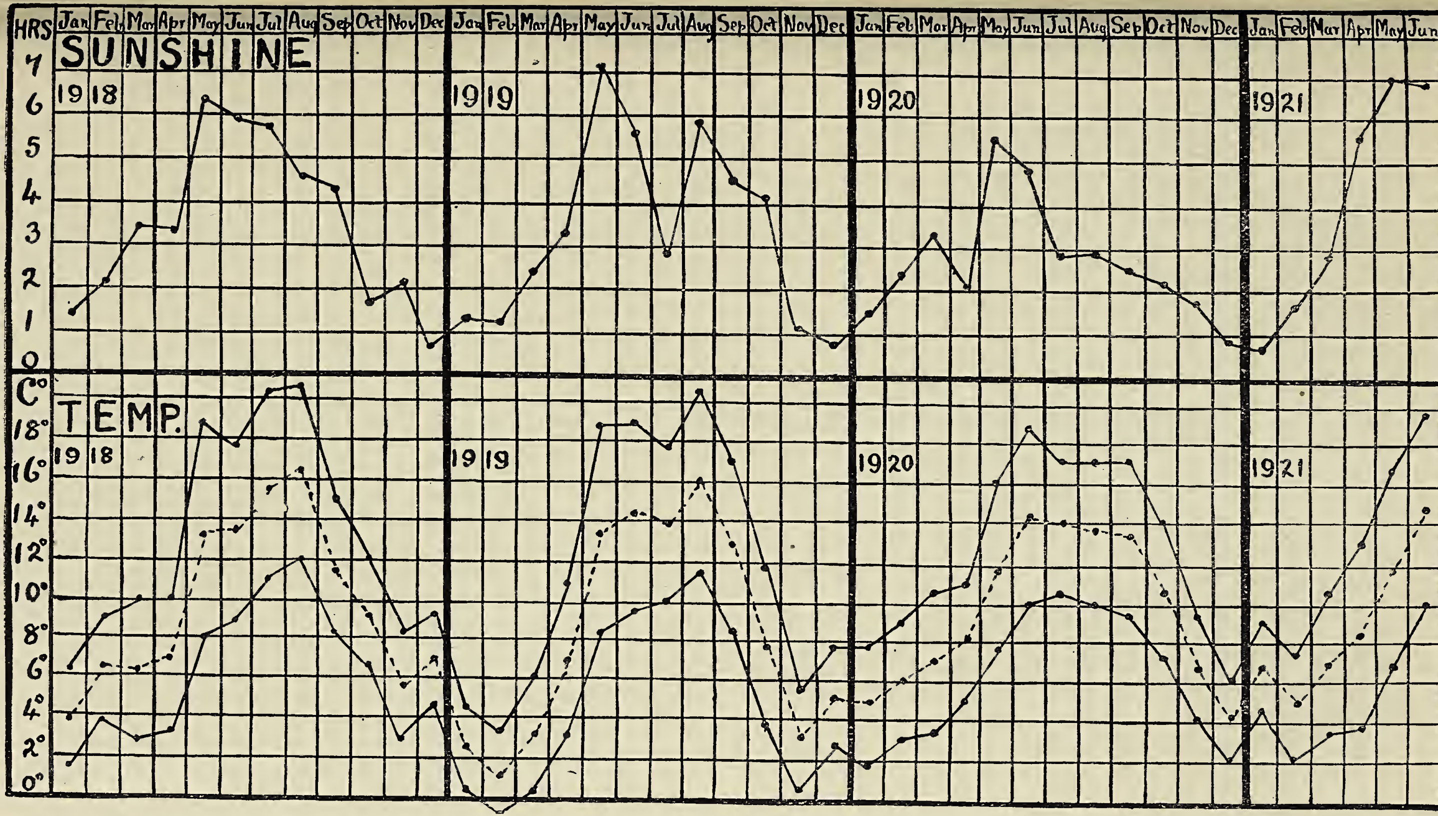

Fig. 2. The topmost curve shows the daily mean, in hours, of bright sunshine for each month. Of the three temperature-curves in the lower half of the figure the uppermost gives the average maximum temperature of the air (in degrees Centigrade), the lowest curve the average minimum, for each month, while the middle broken line represents the mean of these two. All the data are from the Monthly Weather Reports (Birmingham Station).

Station)[1]. The average temperature-conditions of the air in the neighbourhood of the pond probably did not differ in any important degree from those which obtained at the Birmingham Observatory.

The sunshine-data (the daily mean, in hours, of bright sunshine for each month) are plotted in the upper part of Fig. 2, while the monthly rainfall (in mms.) is represented in the upper part of Fig. 3, the records in both cases also being taken from the Monthly Weather Reports (Birmingham Station). These curves will frequently be referred to in the detailed discussion of the occurrence of the various algal species which will follow, but several noteworthy points in connection with the weather during the period of observation may be mentioned here. The years 1918 and 1919 were fairly normal, but 1920 was a very abnormal year. The summer of 1920 was characterised by a low temperature, and it was deficient in sunshine; while the winter of 1919–1920 was very mild. In the case of each of the three complete years the sunniest month was May, and the dullest month December.

IV. CONCENTRATION OF THE WATER

With regard to the variations of the water-level of the pond, shown in Fig. 3, the information was obtained from a convenient wooden stake, driven into the bottom of the pond at a short distance from the margin. When the water was at its maximum height a definite length of the stake projected above water, while even at the lowest ebb noted during the period of observation the stake was never completely out of the water, so that by measuring the length of stake above the water, each time the pond was visited, a record of the fluctuation of the water-level was obtained. Of course this method gives far more exact information than vague terms such as "high," "rather low," etc., such as several workers in this connection have used.

It was recognised at the commencement that periodical chemical analysis of the water of the pond would have given data probably of great value in elucidating the various factors controlling the development of the various algal species, but at the time the work was commenced the writer was not in a position to carry out complete chemical analyses. As a substitute the total amount of dissolved matter in the water was determined each month (from June 1918). This was obtained by carefully evaporating to dryness, in a porcelain evaporating dish of known weight, 100 c.c. of the filtered pond-water

[1] Monthly Weather Report of the Meteorological Office, London.

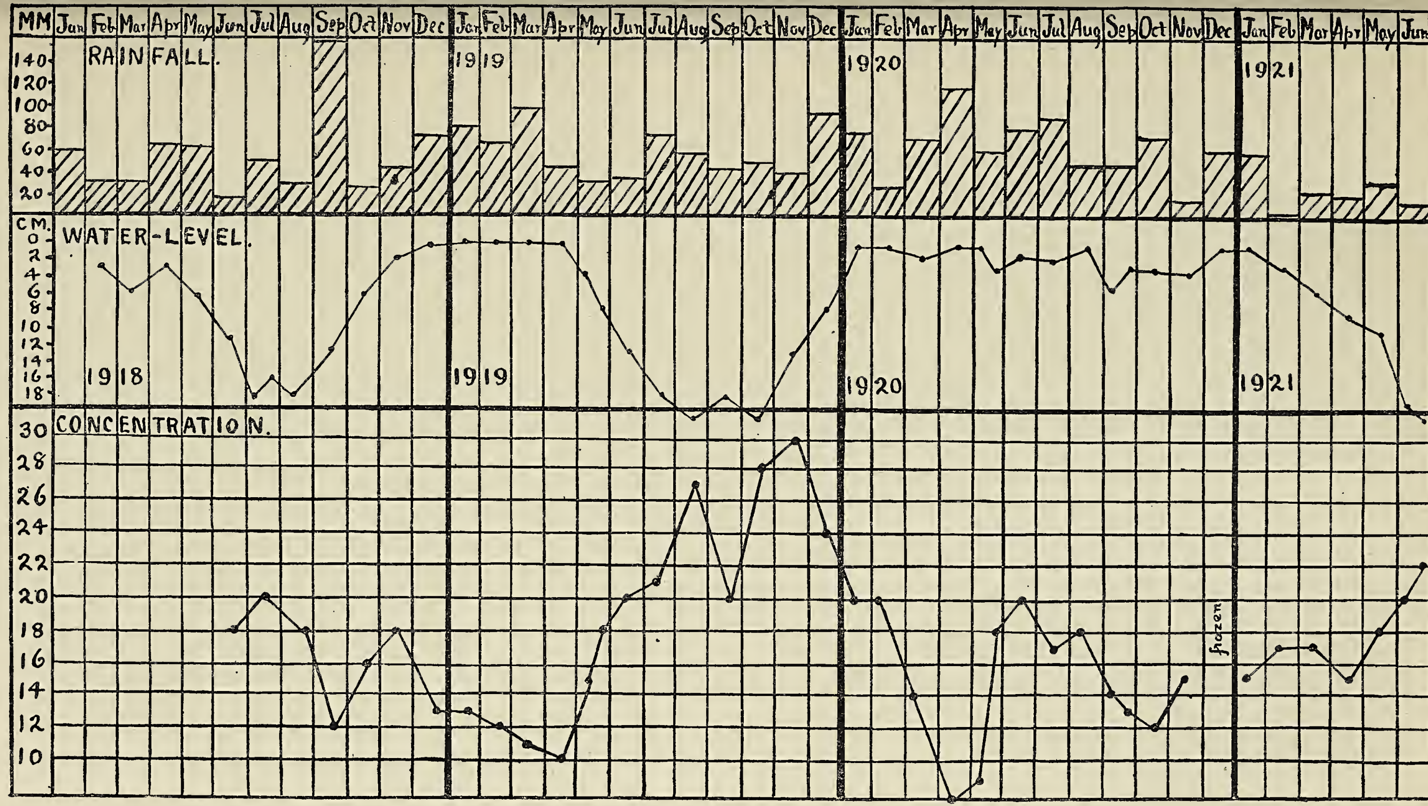

Fig. 3. The rainfall-data at the top of the figure give the monthly rainfall in millimetres (data from Monthly Weather Reports, Birmingham Station). The middle curve shows the height of the water of Hawkesley Hall Pond for each month (in centimetres) below the maximum height attainable. The lowest curve represents the variation in the total amount of dissolved matter in the water of Hawkesley Hall Pond, the figures being "degrees" (parts per 100,000 of water). See Section IV for further details.

(obtained at the time the monthly samples were collected) over a steam-bath and weighing the dish with its residue[1].

It will be seen on reference to the lowest curve of Fig. 3, where the results, in parts per 100,000 parts of water (in the sequel termed "degrees")[2], are plotted, that the total dissolved matter in the water varied during the $3\frac{1}{2}$ years between rather wide limits, namely between 8 and 30 degrees. A comparison of this concentration-curve with the curve showing the fluctuations in the water-level, and also with the rainfall data (all given in Fig. 3), reveals several interesting and somewhat unexpected results. In the first place the lowest concentration in both 1919 and 1920 was reached in the month of April, a result of the dilution of the pond by the winter and early spring rains. As one would rather expect, the two curves of Fig. 3 to a great extent vary inversely, the periods of low water-level generally corresponding to high concentrations, and *vice versa*, this being very obvious in the latter half of 1919; but this is not always the case, and in the autumn months especially the water-level is often rising at the same time as the concentration of the water is increasing.

Thus from September 21st to October 19th, 1918, the water rose 6·2 cm. but the dissolved matter in the water between the same dates increased from 12 to 16 degrees; and notwithstanding a further rise in the water-level of 3·8 cm. between October 19th and November 16th the concentration had increased to 18 degrees by the latter date. Again from October 18th to November 22nd, 1919, the level of the water rose 8 cm., but the dissolved matter of the water also increased from 28 to 30 degrees. During the autumn of 1920 the phenomenon of the concentration increasing with a rising water-level was not shown so well, since the water-level was fairly constant between September and November, but even so the concentration showed a decided increase between October and November.

It is obvious, therefore, that a correct idea of the variation of the concentration of the water cannot be obtained merely from an examination of the fluctuations of the water-level of a pond, and

[1] The same dish was used throughout, and it was kept specially for this purpose, never being used for any other work. After evaporating the water to dryness the dish with the residue was allowed to cool in a desiccator, and was then carefully weighed, using a chemical balance sensitive to a milligram. It was found that the weighing process had to be carried out rather quickly since the deposit was very hygroscopic and rapidly absorbed moisture from the air, an exposure of a minute or so to the air being sufficient to alter its weight appreciably.

[2] It is convenient to term one part of dissolved matter in 100,000 parts of water a concentration of one "degree." The term thus falls in with the chemist's "degree of hardness."

still less from the rainfall data alone. In the case of the present pond the question at once arises, how is it that during certain months the concentration may be increasing when the water-level is rising? It has already been mentioned in Section II that during the autumn the very considerable quantity of floating leaves of *Potamogeton natans* are in process of decay, and there seems no doubt that the products of this decay, which must be considerable and which of course are returned to the water, are responsible for the marked increase in dissolved matter noted during October—November 1920, and September—November 1918 and 1919. Moreover, as will be referred to later in Section V, during the autumn months (September—November) very considerable masses of *Œdogonium*, growing between the leaves of the *Potamogeton natans*, gradually decay, and the resulting products must also have contributed to the increase in dissolved matter noted during the autumn months.

Later on (in Section V) reference will be made to a great maximum of *Zygnema*, culminating in May (and occurring in all four years), but a quick decline setting in during June, at the end of which month this Alga is generally rare. Now between May 8th and May 29th, 1920, the water-level fell 2·5 cm., while the concentration at the same time increased from 9 to 18 degrees—an amount which it seems impossible to account for by the mere evaporation of the water; and from May 29th to June 17th of the same year the water-level rose 1·3 cm., but notwithstanding this dilution the concentration increased still further to 20 degrees. There is some evidence, therefore, that the products of the decay of *Zygnema* are partly responsible for this increase in dissolved matter observed during May and June, 1920. During these months in 1919 the water-level was falling, so that it is not possible to say how far the rising curve of dissolved substances was the result of decay of Algæ, or of mere evaporation.

It will be convenient here to refer to some periodic determinations of the freezing-point of pond-water made by Transeau (28) during 1913–1915. He states that his results "indicate that the highest concentrations coincide with the periods of greatest rainfall and higher water-levels, and the periods of low concentration are coincident with low water-levels and drought" (*l.c.* p. 131). He considers that these results are due to the rains bringing in soluble salts from the upper layers of the soil, and by the silt, clay and suspensoids, also brought in by the rains, slowly settling to the bottom of the pond and carrying "nearly all the soluble salts with them." He limits this statement to "pools, ponds and streams fed by surface run-off,"

and mentions that the underground water of a well gave opposite results.

These conclusions certainly do not apply to Hawkesley Hall Pond (which nevertheless receives most if not all of its water from surface-drainage of the land), as even a cursory examination of the curves of Fig. 3 will show; and even in the cases noted where the concentration of the water increases simultaneously with a rise of the water-level, the explanation put forward by Transeau in the case of the American ponds is not adequate to explain the facts in the present instance. Of course it must be borne in mind that the amount of soluble matter carried into a pond by drainage-water depends very largely upon the geological nature of the rock-strata in the neighbourhood of the pond; and this fact alone would very seriously interfere with the general applicability of the results obtained from Transeau's examination of ponds in central Illinois.

From what has been said already there is reason to believe that the water of Hawkesley Hall Pond contains rather large amounts of organic matter in the form of soluble peaty compounds resulting from the decay of the various phanerogamic and algal species, and a few determinations were carried out to ascertain roughly the proportion of these organic substances to the inorganic salts in the water.

With regard to the hardness of the water of the pond, which was determined[1] each month from June 1920 onwards, the following table gives the results obtained:

Table showing the Degrees of Hardness[2] of the Water of Hawkesley Hall Pond from June 1920 to June 1921.

	1920							1921					
	May 29	June 17	July 15	Aug. 7	Sept. 18	Oct. 16	Nov. 13	Jan. 8	Feb. 12	March 12	April 16	May 14	June 11
Temporary Hardness	3·5	3·3	3·3	3·8	3·9	3·9	3·8	3·6	3·4	3·5	3·6	4·0	4·5
Permanent Hardness	0·5	0·5	0·5	0·6	0·6	0·6	0·6	0·5	0·5	0·5	0·5	0·6	0·6
Total Hardness	4·0	3·8	3·8	4·4	4·5	4·5	4·4	4·1	3·9	4·0	4·1	4·6	5·1

From this table it is obvious that the hardness of the water between May 1920 and June 1921 tended to remain remarkably constant, so

[1] By Hehner's method, as described, for instance, in Newth's *Manual of Chemical Analysis*, p. 328.

[2] Temporary hardness is due to calcium or magnesium carbonate, permanent hardness to (mainly) calcium or magnesium sulphate. A degree of hardness is equivalent to 1 part of $CaCO_3$ in 100,000 parts of water.

that the rather wide fluctuations (between 12 and 20 degrees) in the total amount of dissolved matter of the water (Fig. 3) during these dates is very probably due for the most part to variations in the quantity of dissolved organic matter, and not of the inorganic salts.

A single experiment was made to determine roughly the amount of organic matter in the water by the method of ignition[1]. On September 18th, 1920, a known weight of the deposit, obtained by evaporation over a steam-bath in the ordinary way, was heated to redness on a piece of platinum foil, and the loss in weight ascertained by weighing. The original weight of the deposit was 0·026 gram, the residue after ignition weighed 0·010 gram, the loss in weight (representing chiefly organic matter) thus being 0·016 gram; or, in percentages, roughly 61·5 per cent. organic matter and 38·5 per cent. inorganic salts. On the same date the total amount of dissolved matter was 13 degrees (= 0·013 per cent.), and from the above experiment we see that roughly 8 degrees of this represents dissolved organic substances, and 5 degrees inorganic salts. Now since on this date the total hardness of the water (by the acidimetric method) was 4·5 degrees there remains only 0·5 degree to be reckoned as inorganic salts other than those responsible for the "hardness" of the water.

Thus it is probably correct to say that only 0·2 to 0·4 of the deposit, as obtained each month by evaporation over the water-bath, was composed of inorganic salts, the rest being organic matter; and that while the inorganic part of the deposit varied from month to month apparently between comparatively narrow limits, the amount of organic matter fluctuated between much wider limits; so that the marked variation observed in the total dissolved matter of the water during the period of observation is mainly to be accounted for by this rise and fall in the amount of soluble organic matter.

V. THE ALGAL FLORA OF HAWKESLEY HALL POND

The pond is very rich in species of Algæ, and the list has been divided into three groups: (1) those Algæ which at certain times have formed a really conspicuous feature of the algal vegetation of the pond; (2) those which have developed at times only to a moderate extent, or have been only locally common at times; and (3) those which have been rare or of isolated occurrence.

Group I includes: *Cryptomonas ovata*, *Trachelomonas volvocina*, *Chlamydomonas Reinhardi*, *Eudorina elegans*, *Pandorina Morum*,

[1] This method, of course, is not very accurate for the determination of organic matter in water, but it will serve to give a rough idea.

Dictyosphaerium Ehrenbergianum, Tribonema bombycinum and its forma *minor, Œdogonium cryptoporum, Œ. crispum*, and other species in the vegetative condition, *Spirogyra calospora* (=*protecta*), *S. inflata, S. colligata* (20), *Zygnema* sp., *Hyalotheca dissiliens, Cosmarium Botrytis, Staurastrum brevispinum, S. Dickiei, Xanthidium antilopæum, Closterium striolatum, C. moniliferum, Anabæna oscillarioides.*

GROUP 2 contains: *Trachelomonas hispida, Synura uvella, Volvox aureus, Scenedesmus denticulatus* var. *linearis, Ankistrodesmus falcatus*, and its vars. *acicularis*, and *spirilliformis, Pediastrum Boryanum, P. tetras, Cœlastrum sphæricum, Chætophora pisiformis, Draparnaldia glomerata, Aphanochæte repens, Tribonema affine, Vaucheria aversa, Œdogonium Borisianum, Œ. Braunii, Œ. echinospermum, Mougeotia scalaris, M. viridis, Spirogyra catenæformis, S. longata, S. nitida, Sphærozosma granulatum, Pleurotænium Ehrenbergii, Staurastrum furcigerum, Closterium Dianæ, C. acerosum, C. Kützingii, C. lineatum, Oscillatoria tenuis, O. splendida, Phormidium uncinatum, P. molle, Cylindrospermum majus.*

GROUP 3 includes: *Euglena viridis, E. sanguinea, E. spirogyra, E. tripteris, Phacus pleuronectes, P. longicauda, P. pyrum, Trachelomonas oblonga, Chlamydomonas Debaryana, C. monadina, Gonium sociale, G. pectorale, Tetraëdron minimum, Oocystis solitaria, Glœocystis gigas, Characium longipes, Apiocystis Braunii, Microspora floccosa, M. stagnorum, Coleochæte scutata, C. Nitellarum, Vaucheria sessilis, Œdogonium rugulosum, Bulbochæte minor, B. intermedia, Spirogyra condensata, S. varians, S. Jurgensii, S. mirabilis, S. Weberi, S. maxima, S. bellis, S. Grevilleana, Cosmarium reniforme, C. impressulum, C. præmorsum, C. Regnellii, Staurastrum inflexum, Penium Navicula, Arthrodesmus convergens, Closterium aciculare, Cl. Leibleinii, Cl. Ehrenbergii, Cl. rostratum, Cl. Venus, Gonatozygon Kinahani, G. monotænium, Arthrospira Jenneri, Tolypothrix lanata, Merismopedia elegans, Amphipleura pellucida, Synedra Ulna, S. radians, Fragillaria capucina, F. mutabilis, Tabellaria fenestrata, Gomphonema parvulum, G. acuminatum, Epithemia turgida, Nitzschia Palea, N. acicularis, Navicula viridis, N. vulpina, N. major, N. mesolepta, N. cryptocephala, Stauroneis anceps, S. Phœnicenteron, Cocconema gastroides, C. Cistula, Amphora ovalis, Cyclotella Meneghiniana.*

VI. GENERAL ACCOUNT OF THE ANNUAL CYCLE OF THE PREDOMINANT ALGAL SPECIES

It has been found convenient to consider the whole algal vegetation of the pond as inhabiting two more or less distinct provinces,

these being (1) the central region of the pond, corresponding roughly with the central area of *Potamogeton natans* (see Section II), and (2) the peripheral region of shallow water. The second region is more especially developed on the east side of the pond (cf. Fig. 1) where the bottom slopes very gradually, producing a rather wide marshy zone of shallow water, which at times is particularly favourable for the development of many algal species.

The Algæ of these two provinces are for the most part remarkably distinct throughout the greater part of the year, although of course there is no marked line of separation between the two regions, and many species are found in both, although the dominant Algæ in the two provinces are generally different. It is not considered that the algal vegetation of all small ponds exhibits this distinction; it only happens to obtain in the present case.

Two communities may thus be distinguished in the algal vegetation, namely a Central Community inhabiting the deeper water, and a Shallow-water Community[1] near the sides of the pond. In the Central Province of the deeper water four phases may be distinguished in the annual cycle, these phases corresponding roughly with the four seasons, although the spring- and summer-phases are the most marked. These four phases are:

(*a*) a Spring-phase (February to May) with *Zygnema* the dominant species;

(*b*) a Summer-phase (June to August) with *Œdogonium* dominant, and *Anabæna oscillarioides* common (but *Zygnema* rare);

(*c*) an Autumn-phase (September to November) marked by a decided decrease in *Œdogonium* and a slight increase in *Zygnema*; and

(*d*) a Winter-phase (December to January), transitional in character, with filamentous Algæ generally scarce, but *Zygnema* usually commoner than *Œdogonium*.

The *Zygnema* (see Section VIII) usually increases rapidly during February, and by May has attained a great maximum, masses of the Alga occupying nearly all the free water-surface between the floating leaves of *Potamogeton natans*. During the spring, however, a wide species of *Œdogonium* (see Section X) gradually increases in amount and by June replaces the *Zygnema*, which rapidly declines during this month. From June to August *Œdogonium* is at a maximum, and is often even more abundant than was the *Zygnema* in spring; while *Anabæna* is usually common amongst the *Œdogonium*

[1] At certain times of the year several more or less distinct communities or facies may be distinguished in this shallow-water region.

during July and August. In the autumn *Œdogonium* gradually decreases in amount, and by November has generally become rather scarce; but the *Zygnema* again develops during September and October, and in general shows a steady increase up to the following spring maximum.

In the Shallow-water Province, however, rather more species are concerned in the annual cycle. Roughly three phases can be distinguished each year, and of these the spring-phase coincides (as regards the season) with the spring-phase observed in the Central Province. The three phases are:

(*a*) a Spring-phase (February to May) with *Spirogyra* spp. predominating, and *Tribonema bombycinum* gradually decreasing, while *Mougeotia scalaris* may be locally common during May;

(*b*) a Summer-phase (June to September) with *Anabæna*[1] dominant, and *Cylindrospermum* locally common; and

(*c*) a late Autumn and Winter-phase (October to January) with *Tribonema bombycinum* the chief species, while *Spirogyra* spp. may be locally common, and *Microspora* more or less developed during the winter.

There is much more variation in the annual cycle shown by the Algæ of the shallow marginal region than in that observed in the Central Province of the pond, and this variation can in many cases be explained by a consideration of the various factors (temperature, concentration of the water, bright sunshine, etc.) which control to a large extent the growth of freshwater Algæ in nature. This matter will be discussed in the following sections.

Perhaps the most obvious point of distinction between the general annual cycle of the algal vegetation of Hawkesley Hall Pond and that described by Fritsch and Rich, both in the case of Abbot's Pool (17) and also Barton's Pond (18), is the absence of any distinct Diatom-phase during the colder months in the pond now under consideration. Diatoms never played more than a mere subsidiary part in Hawkesley Hall Pond, although a fair number of species were observed in it.

The more detailed discussion of the periodicity of the chief algal forms represented in the pond now comes under consideration.

[1] *Anabæna* also extends into the deeper water during the summer months.

(*To be continued.*)

THALASSIOPHYTA AND THE ALGAL ANCESTRY OF THE HIGHER PLANTS[1]

By F. E. FRITSCH

The publication by Church in 1919 of his "Thalassiophyta and the Subaerial Transmigration[2]" introduces in the main two new aspects in connection with the origin of land-plants. The first of these substitutes for the old view of invasion of the land *viâ* rivers and other pieces of freshwater, a conception of direct evolution from Seaweeds gradually becoming adapted to terrestrial conditions as they were left exposed on rising sea-bottom. The second hypothecates that the first land-plants originated, not from simple filamentous Algae, but from bulky Seaweeds of some considerable dimensions, exhibiting oogamy and fertilisation *in situ* and possessed of a regular alternation between an asexual diploid and a sexual haploid phase. Church's fascinating memoir deals at great length with these two theories and all that they involve, and numerous facts are adduced in their support. At the same time it seems to me that not all the available ground has been explored and that, particularly as regards the second concept, there are certain facts which indicate the possibility of a different conclusion.

It is generally agreed that the precursors of terrestrial plants must have been green, starch-producing Algae (cf. Church, *loc. cit.* p. 88), since other lines of Seaweeds possess a photosynthetic mechanism which does not appear to have been successful on land. Green Algae (apart from the highly specialised line of the Siphonales), however, play a relatively subordinate part in the sea, both as regards number of species and individuals. Moreover no Green Alga has attained to any really considerable dimensions or bulky parenchymatous construction, and it is significant that in this respect there is nothing to choose between freshwater and marine Cladophoraceae or Ulvaceae. In fact it may be said that Chlorophyceae as a whole possess no somatic organisation such as has been evolved

[1] From the Botanical Department, East London College, University of London.

[2] *Oxford Botanical Memoirs*, No. 3.

by the Phaeophyceae and Florideae. The same statements apply to the Cyanophyceae and, except as regards relative abundance, also to the Diatoms[1]. In short all those phyla which have been really successful in freshwater and terrestrial habitats exhibit no greater development in the sea than on land and are in fact, except in the case of Diatoms, relatively poorly represented in the former. Even the Siphonales, which exhibit a comparatively high vegetative development, are, in their reproductive features, on a lower plane of development than many Brown and all Red forms and in this respect are at a lower level than the freshwater representatives. These, *Vaucheria* and *Dichotomosiphon*, are the only oogamous members of the series[2]. Such forms as *Trentepohlia*, *Draparnaldia*, and *Coleochaete*, in one feature or another, show indications of higher equipment than is found in any marine Green Alga.

In view of the dominance of Chlorophyceae and Cyanophyceae in freshwater and terrestrial habitats it appears warranted to conclude that for them conditions of life in such situations have been more favourable than in the sea, where perhaps they have been unable to hold their own against the more successful Brown and Red forms. These latter do not appear to take kindly to freshwater, and such few examples as are known (*Hildenbrandtia*, *Lemanea*, *Batrachospermum*, *Lithoderma*, etc.) are largely characteristic of rapid streams, many of the Red forms betraying their extreme light-sensitiveness by frequenting the underside of overhanging rocks and other shaded habitats. There is considerable probability in these cases of direct estuarine migration (Church, *loc. cit.* p. 8).

Church holds the view that "the Green Algae surviving in freshwater are somatically the merest depauperated relics in the last phases of deterioration, as reduced filamentous and disc-types" (p. 8). Presumably he would apply the same explanation to the Blue-green Algae, for on p. 32 he speaks of "the flora of freshwater ponds and freshwater Algae, presenting types of organism so far removed from their original condition." That series of reduction of filamentous forms can be recognised in some of the lines of Chlorophyceae is unquestionable, but there is no evidence of reduction in the group as a whole, that is to say there is nothing to show reduction from forms organised on a higher somatic basis. The groups Chloro-

[1] Church (*loc. cit.* p. 47) cites the marine *Schizonemas* and *Licmophora* as instances of higher organisation amongst marine Diatoms, but the difference as compared with some of the freshwater colonial forms is not very great.

[2] *Sphaeroplea* might be added, but it is doubtful whether it belongs to this series.

phyceae and Cyanophyceae can equally well be regarded as having remained at a low horizon of development.

It may moreover be pertinently asked in this connection why, if freshwater Algae are reduced, the marine Chlorophyceae (and Cyanophyceae)—in what Church considers to be the more favourable environment—do not exhibit any higher organisation than their freshwater allies. Church (p. 30) contrasts the freshwater *Vaucheria* with the marine *Codium*, the former being regarded as having a reduced thallus, but, apart from the absence of all evidence of reduction, there are a considerable number of marine Codiaceae (*Aurainvillea, Udotea minima*) in which the organisation of the thallus is not much in advance of a *Vaucheria* or *Dichotomosiphon*[1]. As far as I am aware too, there is nothing to choose between the marine and freshwater Phanerogams, either as regards dimensions or prolific growth. In short a comparison of the existing forms which grow in both types of habitats far from supporting the view advanced by Church seems to indicate that conditions of plant-growth in the sea are less favourable for green plants than in freshwater.

Church points out (p. 7) that the chemical content of fresh as opposed to salt water is strikingly inferior, a fact about which there can be no difference of opinion, but this does not necessarily imply that nutrition is or was easier in salt than in freshwater. Too little is known about the nutrition of Seaweeds to enable one to express an opinion on the point[2]. Moreover it may be doubted if we can safely assume that the primeval sea was at all as rich in mineral salts as that at the present day; according to Schuchert[3] "the Archeozoic oceans had far less salts and probably a different salt combination." The change from marine to freshwater conditions in those remote times may not have been anything like as pronounced a one as it would be at the present day and this may perhaps be the clue to the reason why transmigration has not occurred in more recent epochs, modern Seaweeds being too highly adapted to their

[1] Church (cf. *loc. cit.* pp. 34, 46) accepts West's view that the Desmids, certainly among the more successful and ubiquitous Green Algae, are reduced from filamentous forms. It has however repeatedly been pointed out (Tansley, in *New Phytol.* **4**, 1905, p. 145; Fritsch, in *New Phytol.* **16**, 1919, p. 5) that all the evidence cited in favour of this view will read equally well the other way. Few algologists would follow Church (p. 8) in regarding *Hydrurus* as a reduced filamentous type.

[2] On the whole Green Algae are more accommodating as regards considerable variations in the concentration of the surrounding medium than the true Seaweeds (cf. for instance Oltmanns' *Morph. u. Biol. d. Algen*, **2**, 1905, p. 178).

[3] *New Phytol.* **19**, 1920, p. 274.

concentrated environment to withstand so radical a change (cf. also p. 178).

Much of the evidence cited by Church as illustrating malnutrition in freshwater is open to a different interpretation. The relevant features of estuarine and salt-marsh vegetation, which he (p. 7) attributes to withdrawal from the open sea, may equally well be a result of the frequent changes in concentration of the medium owing to tidal influence. The statement that "all freshwater Plankton is on a lower plane in size, variety, and abundance" (footnote 4 on p. 7) is also open to question. There is no doubt a difference as regards size, but is that not more plainly related to the greater buoyant power of sea-water? As regards variety, however, it may be doubted if there is any appreciable difference, and under certain circumstances, as in warm waters (especially Tropics[1]), the abundance of freshwater Plankton may quite well equal that customary in the sea.

It does not appear therefore that there are any adequate grounds for the views (*a*) that conditions in freshwater are necessarily less favourable to growth than those in salt water, or (*b*) that freshwater Algae as a whole are reduced forms. It is however a striking fact that all Green Algae (excl. Siphonales) leave off abruptly at a level of morphological development which is far inferior to that exhibited by the true Seaweeds. It is at least a plausible assumption that Green Algae do not pass beyond this level, because all the more advanced forms have progressed landwards and given rise to the higher land-plants. They alone (likewise the Cyanophyceae) seem to have found more suitable conditions on the land and in freshwater than in the sea. The conclusion is that the transmigrant Green Alga was at about the level or perhaps slightly above the level of the present-day forms, at least in morphological development. The absence of more advanced forms in the series of the Green Algae is, on this basis, explained as due to failure to compete successfully in the sea with the Brown and Red forms and, for the rest, to their evolution into land-plants.

It is particularly to be noticed that Green Algae (as also Cyanophyceae and to a lesser extent Diatoms) show a very marked power of adaptation to life on land. In practically every series of Green Algae, as at present distinguished, there are terrestrial representatives, as illustrated by the following epitome:

Tetrasporales: species of *Palmella* and *Gloeocystis*.

[1] Cf. Fritsch, *Proc. Roy. Soc. London*. Ser. B. **79**, 1907, p. 220.

Protococcales: numerous forms (species of *Chlorococcum, Chlorella, Trochiscia*, etc.).

Ulotrichales: species of *Hormidium, Prasiola, Stichococcus, Microspora, Rhizoclonium.*

Chaetophorales: *Trentepohlia* and other members of Trentepohliaceae; *Pleurococcus* (?).

Oedogoniales: *Oedocladium.*

Siphonales: *Vaucheria.*

Conjugatae: species of *Mesotaenium* and *Cylindrocystis*; *Zygogonium ericetorum.* (See also Bristol, *Ann. of Bot.* **34**, 1920, p. 35.)

The extent to which such terrestrial Algae are developed is probably not generally familiar. Everyone is of course acquainted with the ubiquity and abundance of *Pleurococcus*, but *Zygogonium ericetorum, Hormidium flaccidum*, species of *Prasiola*, and species of *Trentepohlia* are scarcely less common and the first-named at least often covers whole acres of ground[1]. On the other hand I know of no records of indubitable Brown or Red Algae as inhabiting equivalent terrestrial situations. Where conditions are less favourable to the growth of Green Algae it is Cyanophyceae that dominate as terrestrial algal forms[2].

A large number of these terrestrial Chlorophyceae and Cyanophyceae possess a faculty for resisting drought, without any assumption of special resting-stages, that is only paralleled elsewhere among Lichens and Mosses[3]. It is certainly not the bulky parenchymatous forms at the present day that are best equipped to resist desiccation. If Church cites *Pelvetia* and the *Fuci* of salt-marshes as instances of bulky forms able to maintain themselves in semi-aquatic environment (p. 21), the numerous terrestrial *Trentepohlias* and other terrestrial forms, such as *Prasiola, Hormidium*, and *Zygogonium*, show the great capacity of filamentous Green Algae to maintain themselves, *even in a dry atmosphere*. The terrestrial Green Alga is indeed highly adapted to its conditions of life and it may have been this faculty, apparently possessed otherwise only by the Blue-green Algae and some Diatoms, that primarily resulted in the success of Green forms in establishing themselves on dry land.

A leading hypothesis in Church's theory may be summarised in his own words (p. 33): "The whole of the fundamental framework

[1] Recent Antarctic exploration has shown that *Prasiola* is probably the most important green plant in the land-vegetation of these latitudes.

[2] Fritsch, *loc. cit.* p. 203 et seq.

[3] Cf. West and Starkey, in *New Phytol.* **14**, 1915, p. 201; Piercy, in *Annals of Botany*, **31**, 1917, p. 527 et seq.; Fritsch, in *Annals of Botany* (in the press).

of the organisation of a land-plant, the anatomy of its tissues, the morphological differentiation of members, as also the otherwise wholly inexplicable sequence of sexual and asexual phases in the life-cycle, are the expression of response to the conditions of marine environment." It is difficult to conceive of any factor or group of factors in marine environment that could be interpreted as especially stimulating evolution in these directions. Is it not more likely that the equipment evolved alike in the sea and in the land-flora is an expression of the general trend of evolution in vegetable organisms? Among Seaweeds (Siphonales, Ectocarpales, Florideae) a massive soma has been evolved from the primitive filamentous condition by several different methods, and are we to suppose that marine environment alone stimulates such evolution and that an analogous origin from simple filamentous forms would be impossible on land? As regards morphological differentiation of members, a flattening of certain portions of the shoot-system for purposes of photo-synthesis is surely a response which can be postulated as readily under terrestrial as marine conditions, and is indeed observed in many "xerophytes" as cladodes and phyllodes, undoubtedly evolved on the land; such flattening is moreover evident in the terrestrial *Prasiolae*. Development of branches (axillary only in Phanerogams and a few others), in close connection with such foliar expanses, is probably a necessary physiological consequence of the localised assimilatory activity. A somatic main axis once established, its downward growth into the soil as a root is not difficult to conceive without the necessity of supposing a derivation from the "crampons" of present-day Seaweeds. If *Rhynia* and *Psilophyton* are to be regarded as primitive Pteridophyta, it is possible that in some of the transmigrant races at least the establishment of roots and leaves was deferred to a fairly late stage.

An alternation between sexual and asexual phases must have come about as soon as the reduction-division became associated with spore-formation, for when the spores were haploid the plant to which they gave rise (gametophyte) was cytologically different from the other (sporophyte). Need we assume that such relegation of the reduction-division to the time of spore-formation could only occur in the sea? There does not appear to be any logical reason for such an assumption, since we know of nothing in marine environment that would specially favour such a direction of evolution. The fact that it exists in many Brown and Red Algae may be taken as merely showing that it is an inevitable trend of evolution in all advancing

plant-life. Why the plant, and not the animal, kingdom has adopted this scheme remains unanswerable (cf. also Fucales).

Among the Seaweeds we meet with great diversity in the character of the alternation, a fact which is best exemplified in the Phaeophyceae (cf. *Dictyota* and *Cutleria* for instance). When Church remarks (p. 25) "In all cases of heterothallic differentiation, the individual derived directly from the zygote is the one which begins to diverge from the type, and expresses deterioration," he overlooks Sauvageau's important work on alternation of the Laminariales[1]. Moreover neither the Ectocarpales nor the simple filamentous Green Algae of the sea show this phenomenon. Even among the Red Algae the Nemalionales exhibit a simple type of "antithetic" alternation which is not much removed from that of *Coleochaete* among Green forms, except perhaps in the incidence of the reduction-division. The fact that there may be no alternation in a considerable bulk of Seaweeds and that there is great diversity in the character of such alternation appears to lend support to the view that alternation need not necessarily only have evolved under marine conditions, but has been a phase of evolution of the Vegetable Kingdom.

Although *Coleochaete* is the only green form that exhibits any definite type of alternation, the potentialities for such an alternation are, as will be shown below, quite evidently present[2]. The absence of definite alternation in most Green Algae (of sea and freshwater alike) may be taken to imply either (*a*) that alternation in green plants was evolved subsequent to the adoption of a land-life, or (*b*) that those Green Algae that had already acquired alternation became the successful transmigrants[3].

In Church's memoir, where the primeval ocean is supposed to have existed before there was any dry land, the origin of a terrestrial flora is postulated as occurring in connection with the gradual elevation of vast continental stretches of sea-bottom above the water-level. What evidence have we that when such elevation took place the Benthos had attained to anything like the stage of development that modern Seaweeds exhibit? Church has sketched for us the fascinating picture of the evolution of Benthic from Planktonic forms as the ocean-floor was raised and the sea became locally

[1] Cf. for instance, *Comptes Rendus de l'Acad. d. Sci.* t. **161**, 1915.

[2] Cf. also Fritsch, "The algal ancestry of the higher plants," *New Phytol.* **15**, 1916, p. 233 et seq.

[3] It is however not easy to suppose that in such a case no form exhibiting alternation should have been left behind.

shallower. Assuming the rise to have been more or less continuous, however gradual, would the period of time elapsing between the establishment of a Benthos and the first emergence of land above the surface be anything like sufficient to suppose that the Benthic Seaweeds could have attained to the high stage of development that Church postulates? It seems improbable.

Moreover, according to the geological testimony[1] there was no continuous ocean *ab initio*; there always was land and apparently more of it than at the present day. That being so, there were probably, as in later geological epochs, frequent earth-movements leading, on the one hand, to subsidence of land and, on the other, to elevation of previously submerged sea-bottom. There may thus have been, always accepting Church's theory as to the method of establishment of the land-flora, repeated transmigrations, some of which occurred at a much earlier epoch than others. It may, for example, be suggested that the Blue-green Algae, with their imperfect cytological differentiation, lack of a sexual process, and very simple morphological construction, were transmigrants at an epoch when the evolution of algal life had not passed beyond this horizon. Their world-wide distribution is quite in accord with such a view. The Green Algae, already at a higher stage of development (complete cytological differentiation, sexuality, higher morphological construction), may have adopted terrestrial existence at a much later period, leaving only the siphoneous series to develop vigorously, mainly in the warmer seas. It may be freely granted that there are also possibilities of transmigrations at still later periods, the transmigrants being highly organised Seaweeds as Church supposes. The considerations put forward in the preceding pages do not however appear to lend countenance to this view which moreover necessitates the assumption that at that far distant epoch evolution in Seaweeds had practically completed itself[2] and that there has been no appreciable change since. It may be questioned too whether such highly developed forms, as Church conceives the transmigrants to have been, would adapt themselves as readily to the conditions of a land-life as simpler Algae would.

The changes involved in the assumption of a land-life are very fully considered by Church and, as regards the probable conditions

[1] Schuchert, *loc. cit.* p. 272.

[2] This is the view actually taken by Church, cf. p. 10. His reference to the *Solenoporae* of the Lower Carboniferous is scarcely relevant in this connection, since at that time the land-flora was already highly developed and we know little of the reproductive mechanism of these forms.

to which the transmigrants were subjected, there can be little difference of opinion except as regards illumination and the moisture-content of the air. On these points Church himself is not clear, since on p. 20 he speaks of "a subsaturated atmosphere and a sky of fog and cloud" and on p. 21 of "the brilliance of open sunlight." It is difficult to conceive of any possibility of transmigration, whether by filamentous or more massive forms, unless the air was almost saturated and there was copious rainfall during the greater part of the period. Even if that was so, however, there must have been an appreciable increase in light-intensity for an organism emerging from the water, and it is difficult to follow Church when he suggests (p. 34) that "types with the elaborated factors of such shade-flora (Florideae) will have the better chance of survival under conditions of malnutrition." All recent experimental work goes to show that shade-loving Algae are extremely sensitive to any increase in light intensity.

The most serious problems for the transmigrant must have been water-supply and the maintenance of an erect habit, since it may be doubted (cf. above) whether the change in the nutritive value of the solution was at all as profound as Church supposes[1]. The abundant terrestrial Algae belonging to the successful groups testify to the capacity of these to exist through a period of diminished water-supply and, as above suggested, this capacity may have been one factor that led to their success in transmigration. It may be granted that it is not easy to picture the origin of even the simplest land-plant from a filamentous Alga, but there is no more difficulty in it than in accepting Church's view. The larger the transmigrant the more acute would be the problem of water-supply at first and it is difficult to conceive of the persistence of an erect Alga 3–6 feet long (Church, p. 90), gradually raised out of the water; and if the transmigrant was not erect from the first, it is not easy to comprehend how such a habit could be subsequently attained[2].

It may be that the land- and water-forms of present-day aquatics give us some indication of what the effect of the assumption of the terrestrial mode of life may have been, viz. a general condensation

[1] As regards this point, if freshwater Algae are derived from marine forms and have been able to survive the "malnutrition" involved in the change, why should not similar forms have survived and gradually developed into higher land-plants?

[2] Church (p. 21) cites an observation of Migula's on *Nitella mucronata* growing erect to a height of 10 inches in subsaturated air "with no other mechanical assistance than the turgidity of its non-corticated axial cells," but since such a plant has little weight to support it can scarcely be regarded as affording evidence for his hypothesis.

and dwarfing of parts whereby the exposure of any large surface or the elevation of any part of the thallus into the drier air some little way above the surface was obviated. Such dwarfing may be seen in the spray zone of larger pieces of water at the present day, in the case of *Cladophora*, *Oedogonium*, *Stigeoclonium*, etc. The gradual origin of an erect growth from such short tufted filaments, as they became accustomed to terrestrial conditions, is not as difficult to picture as the persistence of a large erect form.

It is, however, possible that an erect growth was not the most important feature of the transmigrant Alga. In each of the three great series of Algae we encounter a similar central type of organisation, in which the thallus is differentiated into two distinct portions, a prostrate attached dorsiventral base, which not uncommonly possesses a parenchymatous construction, and an "erect" radial portion. This is well exemplified in the species of *Stigeoclonium* and *Trentepohlia* among the Chaetophorales (Chlorophyceae), in *Ectocarpus*, *Cutleria*, etc. among the Phaeophyceae, and in several of the Nemalionales among Florideae. In the Seaweeds such an organisation appears on the whole to be most marked among the simplest members of their respective series, whilst the Chaetophorales, the bulk of which are freshwater or terrestrial, are among the most advanced members of the Green Algae[1]. It seems probable that this type of construction marks a stage in the evolution of the Algae, the highest attained by the Green forms of the present day.

In each of the series just mentioned we find, side by side with forms with a practically equal development of the prostrate and "erect" portions, others in which the one or the other is more or less completely reduced (among Chaetophorales compare *Draparnaldia* and *Protoderma*). In the aquatic Green forms the reproductive organs are usually borne on the upright system, but in some of the terrestrial *Trentepohlias* the spherical sporangia, which have been shown in several cases to be gametangia, are confined to the creeping base[2], whilst the asexual stalked sporangia, so highly evolved for aerial dispersal, are found on the "erect" system. Among Phaeophyceae, in *Myrionema vulgare* and *Cutleria* (in the latter on two distinct generations), the converse is the case. I have previously suggested[3] that the Algae from which land-plants arose possessed

[1] Fritsch, *loc. cit.* p. 235.

[2] Cf. Heering, in Pascher, *Suesswasserfl.* **6**, 1914, Fig. 173, a; De Wildeman, *Algues Buitenzorg*, 1900, p. 72; Schmidle, in Engler's *Bot. Jahrb.* **30**, 1902, p. 63, Tab. II, Figs. 8, 10.

[3] *Loc. cit.* p. 240.

such a thallus developed in two directions (as indeed present-day *Trentepohlias* illustrate) and that as an adaptation to subaerial conditions relegation of the sexual reproductive organs to the creeping base took place. Such a theory is in harmony with the prevalent dorsiventrality of the gametophyte and helps to explain the persistence of "aquatic" fertilisation in Bryophyta and Pteridophyta[1]. Whether alternation was already established or whether it became subsequently established is immaterial; as soon as two phases were evolved they would be bound gradually to diverge, the one (gametophyte) losing the erect system (except in Mosses?), the other (sporophyte) the prostrate system. In the dual development of the primitive type of thallus we have all the potentialities for the evolution of the two highly contrasting phases in the life-cycle of land-plants. On this view they were probably *ab initio* identical.

Let us consider the position of such a filamentous form, as it gradually became exposed by the rising of the land out of the water. Assuming the power of adaptation to terrestrial existence so strongly evidenced by the Green Algae of the present day and the general condensation of the exposed parts above postulated, we should have a dense tufted erect growth (probably of no appreciable height) arising from a creeping basal system which would probably not be as much affected at first at least[2]. Such a form would not be subjected to the vicissitudes to which larger forms would be exposed and, with the more favourable conditions for photo-synthesis and the better oxygen-supply, might well make relatively rapid headway. It is difficult to conjecture what direction the advance might take at first, but there may well have been an early departure from the filamentous condition and the adoption of a more massive habit, either in both parts of the thallus or only in the creeping base. It may be an open question whether the transmigrant Alga had already attained to oogamy. There are no oogamous Green Algae in the sea (cf. Oltmanns, II. p. 176), so that oogamy may either have arisen subsequent to transmigration or the oogamous forms were the successful transmigrants[3]. At whatever stage oogamy may have been evolved fertilisation *in situ* and post-sexual nutrition would be a likely consequence of the increased efficiency of the organism due to the acquisition of a more massive body. It is to be noted that among Seaweeds the features in question are exemplified only in the

[1] Regarding Mosses, see Fritsch, p. 250.

[2] Since probably still periodically inundated.

[3] In the latter case it is however again difficult to conceive that no oogamous forms should have been left behind.

Red Algae, a group so highly specialised that it may be doubted if it is warranted to draw any conclusions from them. On the other hand fertilisation *in situ* is a commonplace among freshwater Green Algae.

Church lays great stress on the fact that a resting thick-walled oospore is unknown among marine Algae, as little as it is found among land-plants above the level of the Thallophyta, whilst the oospores and zygospores of freshwater Algae invariably become equipped with a thick coat and pass through a more or less prolonged resting period. This is certainly a significant feature, but perhaps too much importance may be attached to it. We have to suppose that the asexual reproductive cells gradually acquired these features[1] as they became developed as wind-borne spores, and if they underwent the change why not the zygote? It is at least plausible that a resting stage was temporarily adopted by the zygospores or oospores during transmigration and that, as the thallus became more massive and post-sexual nutrition was initiated, this stage was again lost. A parallel is furnished by the evolution of the seed among higher land-plants, where the presence of a megaspore-membrane in Cycads, Conifers, etc. cannot but be taken as evidence of the former existence of thick-walled spores which, as nutritive devices developed, remained *in situ* and lost the thick membrane. Whilst therefore there is no reason to suppose that the zygotes of Seaweeds ever presented a resting stage (the conditions of life rendering it unnecessary), it is quite possible that such was realised during transmigration and retained as an advantageous device by freshwater Algae liable to desiccation, though subsequently lost in the main lines of landward evolution. Transference of the resting stage to the asexual reproductive units would present little difficulty since many of the simpler Algae (*e.g. Ulothrix, Stigeoclonium*) exhibit the power of initiating asexual resting cells side by side with the resting zygote. In fact the marked capacity for forming resting stages by several different methods (akinetes, aplanospores or encapsuled zoospores, zygotes) may have been another of the factors that led to the success of the green phylum.

A necessary adjunct to a successful terrestrial existence was no doubt the development of a more perfect type of sexual organ such as is exemplified by the archegonia and antheridia of present-day Bryophyta and Pteridophyta, and the preliminary steps in this

[1] In this connection attention may be drawn to the facility with which most freshwater Algae adopt a thick-walled resting condition on the part of structures that do not normally exhibit these features (akinetes, aplanospores, etc.).

direction may well have been taken at an early stage of transmigration. Church is of the opinion that "the archegonium is a derivative only of a truly parenchymatous type of soma" (p. 13), but it may be doubted if that is necessarily the case. *Ectocarpus* shows us how a multiseptate reproductive organ can arise in forms which are in the main monosiphonous and it may be questioned as to how far such a multiseptate organ is really removed from a gametangium of *Ulothrix* or similar form where there is likewise division along several planes, although the resulting units do not become separated by walls. It is not difficult to suppose the gradual evolution of archegonia and antheridia from a gametangium producing a considerable number of gametes, by the gradual modification of those of the peripheral series into a protective cellular wall. But the matter cannot pass beyond the realms of pure speculation and it is possible to visualise a number of different possibilities. There do not however appear to be any grounds for assuming that even a very early prototype of these organs had been evolved prior to transmigration, although that may have been the case.

Church regards the archegonium as being very probably polyphyletic, a view with which one is inclined to sympathise. The regular occurrence of a ventral canal cell seems to me, however, to place considerable difficulties in the way of its adoption and to imply a common ancestry for all archegoniate forms. Such a feature is difficult to explain on a theory of convergence. In supporting a polyphyletic origin for the different groups of land-plants (*e.g.* p. 82) Church places considerable weight on the type of flagellation of the spermatozoids. It may be doubted however if this feature always possesses the importance which is nowadays attributed to it, since several examples of the existence of diverse types of flagellation in one and the same form are known (cf. zoospores and spermatozoids of *Vaucheria* and the two forms of zoospores seen in some Saprolegniaceae). We may not lose sight of the possibility that the type of flagellation may in part be related to external factors of which we at present have little comprehension.

According to Church's theory (p. 89) "The Algae of the transmigration...combined the best features...of the known great conventional series of marine phytobenthon, and yet...belonged to none of them." In other words the Algae that gave rise to the transmigrants have completely disappeared. That is plausible, but it is difficult to understand on this basis why Green Algae (as we find them at the present day) should almost alone have adopted life in

terrestrial and freshwater habitats and should be so poorly represented in the sea. These are facts which speak for a common origin of freshwater and terrestrial Green Algae and the higher land-plants and, since evidence of reduction in Green Algae as a whole cannot be admitted, it strikes at the root of Church's assumption.

At this point reference may be made to the other aspect of Church's theory, viz. the mode of transmigration. According to the present-day geological view there were both land- and sea-surfaces from the earliest times. If that was so, there was no doubt evaporation from the surface of the sea and subsequent atmospheric precipitation, which will have led to the formation of rivers and other large bodies of freshwater. We cannot preclude the possibility of an independent origin of green plant-life in such pieces of freshwater and of the ancestors of the higher plants never having been in the sea at all. Invasion of the sea by way of rivers on the part of a few freshwater Green Algae is not an impossibility and in the case of forms like Cladophoraceae and Ulvaceae even plausible in view of their present-day distribution. I hold no brief for either view, but consider that both possibilities must be reckoned with.

EAST LONDON COLLEGE,
July, 1921.

THE STUDY OF HUMAN IMPLEMENTS AS AN AID TO THE APPRECIATION OF PRINCIPLES OF EVOLUTION AND CLASSIFICATION

By E. J. SALISBURY

Everyone who has attempted to teach the fundamental facts with respect to evolution and principles of classification has probably found the value of concrete examples in elucidating abstract concepts. But whether examples be culled from the animal or vegetable kingdoms there are always preconceptions in the student's mind with regard to them which tend to obscure the principles to be deduced from their study.

To overcome this difficulty the writer has resorted to the use of an analogy which the Editor has asked him to explain in the hope that others may find it equally helpful.

In the choice of such an analogy a wide field is offered us. If for example we wished to illustrate convergent evolution, probably no better examples could be found than the many isotopes which have now been demonstrated by the chemist and physicist possessing apparently identical chemical properties but different atomic weights. The two types of lead derived from uranium and thorium respectively offer as striking an analogy to the convergent evolution of the biologist as could well be found.

So too the morphologically identical Eucalypts, only separable by means of the terpenes which they contain, or the different albino Primulas, only distinguishable when analysed by the geneticist, are paralleled by the isomeric compounds of the organic chemist.

The periodic series into which the chemical elements fall and the light that has been shed by the study of radio-active substances have as profound a significance as the study of the passage from nebula to star and each serves to emphasise a particular aspect of the evolutionary sequence. Recently the former analogy has been developed by Heslop-Harrison in relation to his section-species of *Rosa* (*Trans. N.H.S. Northumberland, Durham and Newcastle*, vol. v, Pt. II, p. 257).

But though there is scarcely a branch of knowledge that cannot contribute something to the comprehension of evolution, especially in detail, the progress of development of man's implements appears

to offer a more valuable analogy with respect to general principles. We have here moreover the material for following the whole course of evolution from the primitive and crude efforts of prehistoric man through all the vicissitudes of increasing complexity and simplification up to modern times. The implement inherits its form by tradition from one generation to the next, whilst each age impresses its environment upon it.

Samuel Butler evidently regarded man's implements in a similar light but attached even more importance to them as the chief avenue of man's evolution (*Lucubratio Ebria*, 1865). To him the stage of man's organisation was measured by the number and variety of these extra-limbs at his disposal. Hence too the rich man was more highly organised than the poor man because of the variety of mechanisms at his command.

When the earliest stone implements are examined we are at once struck by the absence of clearly separable types. It is true these "eoliths" present various forms, but they bear comparatively little evidence of human workmanship and their differences depend rather on the character of the original stone selected than on its subsequent modification. There can be little doubt that these earliest implements served a variety of purposes, their very lack of differentiation rendering this possible. The eoliths are as it were the "Protista" of man's implements with many and various potentialities, some, though not all, of which we find realised in the increasing differentiation of succeeding epochs.

In the implements of the Strépy and Chellaean periods, probably contemporary with Piltdown Man and the presence of the Hippopotamus and Rhinoceros in Europe, human handiwork is much more pronounced, though here again there is but little differentiation. So slight is this indeed that we should probably hesitate to regard them as distinct species were we dealing with biological entities. Here then we find emphasised the first fundamental principle, namely, that specific rank, which is after all an artificial aggregate of convenience, cannot have the same value in a group exhibiting little division of labour, as in one of highly organised units. There is more difference in the absolute sense between the multitudinous types of modern table knives than between the variations in the stone implements of the Chellaean and Acheulaean epochs, yet the distinctions of the former are unlikely to lead to any striking new advances in the evolution of the knife, still less to any entirely new implement. So far as we can judge they have no survival value.

If on the other hand we consider the heavy hand axe of the Chellaean period, coarsely flaked on both faces, and compare it with the "ficron" type with its tapering point and more or less triangular section we realise as we pass to the Moustierian epoch that this type, though so little different from the normal one, was in reality the evolutionary starting-point of the pick-axe and the hand-drill, the origin that is of entirely new classes of implements.

A consideration of such examples helps one to realise that the differences in structure which serve to distinguish species of *Chlamydomonas* or Bacteria are necessarily small as compared with those separating *Capsella heteris* from *Capsella simplex* or *Silene nutans* from *Silene dubia*; yet such small differences in a relatively undifferentiated group, which has not lost its plasticity by division of labour, may be the inception of fundamental evolutionary changes. The value of the character, whether in the organism or organ, must be considered relative to the complexity or simplicity of its organisation.

When we pass from the Chellaean to the Acheulaean period the diminishing size of the flaking involving a higher grade of technique seems a relatively small development, but this increased dexterity made possible the thinner implements of the Moustierian period, with one plane face, which resulted in the marked development of the hafted axe in the split haft. It is in this period too that we find the flint drill and pick well developed whilst the finer flaking has also made possible the flint knife.

Here again the distinction between the newly made knife of primitive man and the one which he had notched with constant use appears a comparatively slight one until we realise that the latter was the initiation of an evolutionary series beginning with the flint saw, and leading on to an entirely new phylum of man's tools, including a variety of implements of abrasion from the cross-cut of the lumberman to the file of the locksmith. So too in the rude scraper of Palaeolithic Man there is little to indicate its manifold derivatives, from the barrasquit d'Espourga, used to shave off the bark in the Landes, or the spokeshave of the wheelwright, to the fillisters and moulding planes of the cabinet-maker.

In the Neolithic period with its enormous advance in technique we find many of the dormant potentialities of the earlier types realised. The knives, picks, and saws had reached a high stage of development whilst the perfection of the boring implements is shown in the perforated stone axe-heads and the eyelet-holes of their bone needles. The hand-axe of earlier periods had already in the Palaeo-

lithic period given place to the hafted axe on the one hand and the spear-head, arrow-head, etc. on the other, all of which attained a much higher development in the Neolithic period.

To the biologist the implements of the Stone age in particular and in a lesser degree those of the Bronze and Iron ages are replete with examples of the importance in evolution of apparently trivial distinctions. As in animate objects, not all of these potentialities develop. In the earliest borers of the Chellaean period we find the "ficron" with curved edges which become straight with the improved technique and finer flaking of the Acheulaean type of borer. Thus a potentiality was lost, not to reappear, as a parallel development in metal, until quite modern times where the borer with the twisted edge finds expression in the high speed twist drill.

We see the forces of natural selection at work in the Neolithic period leading to the sifting out of specialised types in correspondence with the changed conditions consequent upon the replacement of Palaeolithic Man the hunter by Neolithic Man the agriculturalist. The hafted implement attains a high state of development and the so called "adze," probably used as a hoe, makes its appearance.

With the advent of metal an entirely new factor is introduced. It was as it were a profound mutation yet, as with plants and animals, the potentialities are not at first obvious and in the initial stages the evolutionary continuity appears to be scarcely affected by the change. Just as the first motor cars were mere caricatures of their horse drawn predecessors, so too the first bronze celts were mere replicas in metal of their stone prototypes.

The bronze axe was bound in the split short arm of the L-shaped haft and we find the capabilities of the new material first developed in the flange at all four edges, to prevent vertical movements, and in the elaboration of the "stop" or transverse ridge which held the axe from being driven back into the haft by the force of the blows. The final phases of this series are the socketed axe-heads with a vertical septum, clearly derived from completely bent-over flanges, and finally the socketed celt with no septum and a loop through which the binding thongs passed. The latter represents the end of a series which has become extinct but the less specialised palstave survives in the machete of modern days.

The chief effect of the introduction of metal is seen in the lengthening of the sword blades and in the manufacture of slender implements such as pins, needles, etc. The latter made of bone had however already appeared in Palaeolithic times and it is doubtful

whether the advent of metal at first added any new invention to man's implements though it greatly increased their efficiency (the fish-hook may perhaps have been an exception). On the other hand there was a great efflorescence of elaboration in the form of ornamentation. It is indeed quite late on in the period of metal that there appeared implements such as the scissors and its allies which metal alone made possible.

Parallel evolution and reversion have their examples in human implements as in biology. The hand-dagger of iron of the middle ages was essentially a reversion in metal to the hand-axe of the Palaeolithic period, and amongst the examples of incompletely perforated Neolithic axe-heads are specimens in which a central plug demonstrates the use of a type of boring implements which would appear to have lapsed but has reappeared in the "self-centering" bit of the present-day carpenter.

Turning to modern times we find that several of the types represented in the Stone age have become phyla, embracing a vast variety of forms exhibiting every degree of specialisation and complexity. We can see in the stone saw the origin of the band saw, circular saw, fret saw, rip saw, etc., and in the hand-axe the forerunner of the battle-axe, the hatchet, the adze, the hoe, etc.

Consideration of the more complex types of implements emphasises the fact that each new advance is in the nature of an increase in complexity and by a process of survival of the fittest this is followed by a period of simplification. Here too we see the analogy with biological phenomena as also in the origin of new types from the more generalised rather than the highly specialised examples.

When we attempt to classify human implements into species, genera, families, cohorts, phyla, etc., we are presented with much the same difficulties as in the animate kingdoms, despite the advantages which a knowledge of their chronological sequence confers.

How, for example, would one classify the "safety razor"? Is it a derivative of the ordinary razor and therefore to be placed in the same class as the knife and the sword or is it a lineal descendant of the plane and therefore of the hide-scraper of Palaeolithic Man? Or again, is the cooper's drawknife a derivative of the spokeshave which it morphologically resembles or is it a descendant of the hatchet to which it is perhaps more closely akin in function?

What may be regarded as degenerate types which differ in function whilst retaining morphological simplicity are well exemplified by the fish knife, the pallet knife, the butter knife, and many others.

The persistence of primitive types side by side with recent and more complex ones is illustrated by the manufacture of flint implements by the Tasmanian aboriginals till well on into the nineteenth century. Moreover the cause of their survival is the same as that which accounts for the persistence of primitive biological types in the same area, viz. their isolation.

Even in the study of geographical distribution the analogy is not without value, for the origin and spread of man's inventions is well fitted to illustrate the importance of natural barriers or the relation between age and area.

If we consider the series of species presented by the genus *Alstroemeria* in which some have edge-on leaves occupying a profile position whilst others have leaves completely inverted involving a still further twist of the leaf base and accompanied by inversion of the internal structure, one cannot but ask why the apparently more fundamental change has been carried out (viz. complete inversion) rather than attainment of the same end by the apparently simpler course which an untwisting of the leaf base would have involved. For it can scarcely be doubted that *Alstroemeria* originally had a dorsiventral leaf with normal orientation. *Allium ursinum* illustrates the same point, whilst we see it again in the development of cladodes as leaves in place of renewed development of the scale leaves themselves.

Such examples, of which other cases might be cited, suggest a sort of momentum in evolution, a view which would harmonise with orthogenesis as conceived by Eimer. Such a standpoint seems more rational than the passive "law of loss" postulated by Dollo and others but, without arguing the point, it may be mentioned in this connection that man's implements often show a sort of momentum in their evolution which is perhaps not without significance for the students of phylogenetic sequence.

In the foregoing the writer has attempted nothing more than a mere adumbration of the possibilities of this analogy, but it will be evident that it is capable of development according to the needs of the teacher and his facilities for illustrating the analogy by means of suitable museum types. Its value as a teaching instrument largely depends on this latter, but in any circumstances one ventures to think that if students of biology occasionally examined anthropological collections from the evolutionary viewpoint they would find much to stimulate and more upon which to reflect.

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CONTENTS

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PERMEABILITY

By WALTER STILES

CHAPTER V

THE PERMEABILITY OF MEMBRANES

THAT colloids are generally incapable of penetrating into a colloidal system was mentioned at the end of the last chapter, and the incapacity of colloids to diffuse through colloidal membranes[1] is the phenomenon which led Graham to distinguish between colloids, substances which are incapable of passing through such membranes or which do so very slowly, and crystalloids, which pass through these membranes readily. By utilising this principle Graham was able to separate colloids from crystalloids, and so introduced the method of separation and purification of colloids known as dialysis.

The permeability of a membrane depends on the composition of the membrane, but the latter is not equally permeable to all substances. For example, caouchouc allows pyridine to pass through it while water is kept back. When a membrane is in contact with a solution the permeability may, and generally does, differ as regards the solvent and the solute. Thus parchment paper allows water to pass readily, but the solute in the case of an aqueous solution of sucrose diffuses through the membrane very slowly. In speaking of the permeability of a membrane it is thus necessary to define the system with which the membrane is in contact.

A membrane which allows a substance to pass through it readily is said to be *permeable* to the substance, while one which does not

[1] The term "membrane" may be limited to thin solid structures, while the term "film" is used for thin layers of liquid. In biology it is often difficult or impossible to distinguish between solid membranes and liquid films, and the term "membrane" will therefore be used to include films.

allow the substance to pass through it is said to be *impermeable* to the substance.

Although colloids generally cannot diffuse through membranes of colloidal substances, it must be realised that this distinction between colloids and crystalloids is by no means absolute. By varying the membrane and the substance, practically any degree of permeability may be found. Particularly interesting in this

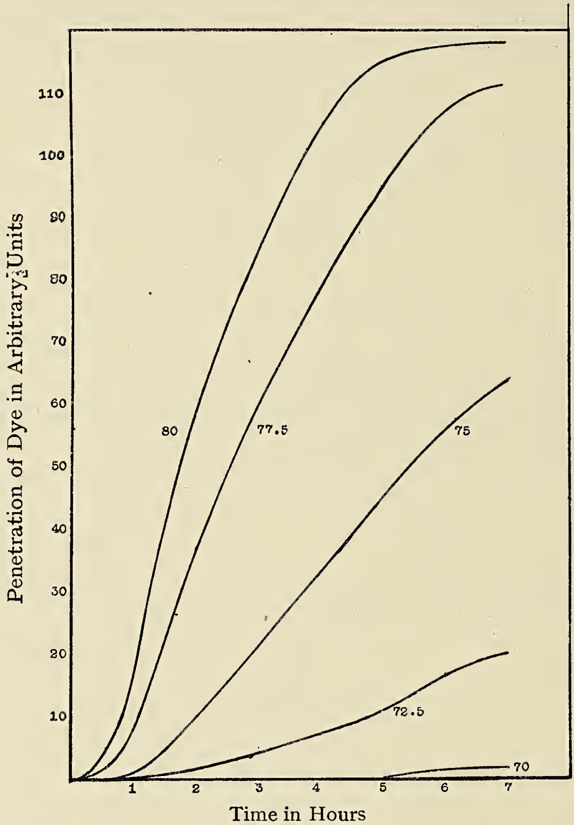


Fig. 3. Curves to illustrate the penetration of methylene blue through collodion thimbles of graded permeability. (Constructed from the data of W. Brown.)

respect are the observations of W. Brown (1915) who describes a method by which membranes of collodion may be prepared of any degree of permeability within certain wide limits. Brown's method consists in preparing completely air-dried membranes of collodion which are highly impermeable. The membranes are then immersed in solutions of alcohol in water for a suitable time. After washing in water the membranes then exhibit a per-

meability which increases with increase in the concentration of alcohol employed.

As an example of the degree of variation in permeability which may be obtained by this method an experiment made by Brown may be cited. Membranes in thimble form of different degrees of permeability were prepared as described by treatment with 70, 72·5, 75, 77·5 and 80 per cent. alcohol respectively. The thimbles were filled with a solution of methylene blue, and immersed in vessels containing distilled water. The amount of diffusion was estimated at daily intervals by colorimetric estimations of methylene blue in the external solution. The curves shown in Fig. 3 are constructed from the data given by Brown. They show what a wide range in permeability is obtained by grading collodion membranes in aqueous solutions of alcohol ranging in concentration from 70 to 80 per cent. As practicable membranes can be obtained by the use of alcohol solutions ranging in concentration from 0 to 97 per cent. it will at once be clear what an extremely wide range of permeability can be obtained at will. The following table gives the values found by Brown for what he calls the "alcohol index" of a number of substances. The alcohol index of a substance is defined as the number which represents the strength of alcohol required to produce a membrane which just prevents diffusion of the substance.

TABLE X

Alcohol Indices of a Number of Substances. (Data from W. Brown)

Substance	Alcohol Index
Water	0
Sodium chloride	0
Potassium permanganate	30–40
Picric acid	35–40
Copper sulphate	60–70
Potassium oxalate	60–70
Sodium sulphate	60–70
Bismarck Brown	65–
Methylene Blue	70–
Neutral Red	72·5–75
Safranin	75–77·5
Dextrin	85–87·5
Starch	90
Aniline Blue	92
Litmus (neutral)	93
Congo Red	96
Night Blue	>96

In a later paper Brown (1917) extends his method for obtaining membranes of graded permeability to other material (gelatine, agar-agar) and a number of grading liquids. Other methods of obtaining membranes of graded permeability are described by Bechhold (1907), Bigelow and Gemberling (1907), Schoep (1911) and Walpole (1915).

When a solution is in question a membrane may be equally permeable to both solvent and solute, or it may be impermeable to both. More frequently the permeability to the two components differs, and generally, in the case of solutions of crystalloids in water, the membranes are permeable to both water and the solute, and more readily to water.

The different rates of diffusion of solvent and solute through a membrane were shown in the first half of the nineteenth century by Dutrochet (1826, 1828, 1840, 1842) and Vierordt (1848) who examined the diffusion of aqueous solutions of salt through membranes of pig's bladder. The water passes through the membrane faster than the dissolved salt, this difference in rate depending on the nature of the salt, its concentration, and, as shown by Graham (1854), on the nature of the membrane.

Graham's discovery of the impermeability of certain membranes to colloids led Moritz Traube to search for a membrane which, while permeable to water, should be impermeable not only to colloids but to crystalloids. Such a membrane, permeable to the solvent but impermeable to any solute may be termed a *semi-permeable* membrane. Although a perfect semi-permeable membrane has never been manufactured, some of the precipitation membranes prepared by Traube (1867) are rather near approximations to one. The best known of these, and the one which has probably been most used, is that of copper ferrocyanide, which is obtained in the form of a gel when solutions of potassium ferrocyanide and copper sulphate come into contact. For most purposes these membranes are too delicate if unsupported, and so they are usually precipitated in the wall of a porous pot, a device due to Pfeffer (1877). Other precipitation membranes are those of glue-tannic acid, copper tannate, lead tannate, ferric ferrocyanide, copper silicate and tin silicate. These membranes, like the collodion membranes already mentioned, are graded in their permeability.

Tammann (1892) investigated the penetration of a number of salts through precipitation membranes of copper ferrocyanide and zinc ferrocyanide. He found the permeability of the two membranes was the same as regards the simple salts he investigated though not in regard to dyes. Traube (1867) had found the copper ferrocyanide membrane permeable to potassium, sodium and ammonium chlorides, and impermeable to barium chloride and nitrate, calcium chloride, potassium sulphate and ammonium sulphate. Tammann, on the contrary, found the membrane permeable to all these salts except calcium chloride. His findings in regard to permeability of the

copper ferrocyanide membrane to a number of salts of the alkali and alkaline earth metals are collected in the following tables.

TABLE XI

Permeability of Precipitation Membranes of Copper Ferrocyanide to a Number of Sulphates. (Data from Tammann)

Salt	Quantity passing through membrane
$(NH_4)_2SO_4$	small quantity
K_2SO_4, Na_2SO_4	smaller quantity
Li_2SO_4	a trace
$MgSO_4$	none

TABLE XII

Permeability of Precipitation Membranes of Copper Ferrocyanide to Chlorides, Bromides and Nitrates of Metals of Alkalies and Alkaline Earths. (An asterisk indicates that traces only pass through the membrane.) (Data from Tammann)

Kation	Anion Chloride	Bromide	Nitrate
Ammonium, Potassium, Sodium, Lithium	All penetrate the membrane in large quantities; much more so than the corresponding sulphates.		
Barium	perm.	perm.*	perm.*
Strontium	perm.*	perm.*	imperm.
Calcium	imperm.	imperm.	imperm.
Magnesium	imperm.	imperm.	imperm.

From quantitative investigations on the diffusion of acids through the copper ferrocyanide membrane, Tammann came to the conclusion that the rate of passage of the acid through the membrane was chiefly dependent on the degree of dissociation of the acid, the more dissociated the acid the more rapid its passage through the membrane.

An investigation by Walden (1892), the results of which were published almost contemporaneously with those of Tammann just quoted, agrees on the whole with these latter. Walden found, however, that membranes of copper ferrocyanide and zinc ferrocyanide had distinctly different permeabilities. Altogether the permeabilities of eleven precipitation membranes to a large number of acids and salts were examined. The membranes employed are recorded in the following table. All these membranes were impermeable to tannin, while all were permeable to the following anions when bound to alkali metal kations (K, Na, ?Li, NH_3): F, Cl, Br, I, CN, CNS, ClO_3, ClO_4, BrO_3, IO_3, NO_2, NO_3, formate, acetate, trichloracetate, iso-

butyrate, valerianate, salicylate, sulphate, thiosulphate, AsO_3, B_4O_7 (the two silicate membranes were not examined in the case of the last four anions). The results with other ions are shown in Table XIII.

TABLE XIII

Permeability of Various Precipitation Membranes to Anions bound to Alkali Metals (K, Na, ?Li, NH_4) (p permeable, i impermeable). (Data from Walden)

	Anion					
Membrane	PO_4	AsO_4	SO_4 (SeO_4)	CrO_4	P_2O_7	Oxalate Ferrocyanide Ferricyanide Cobaltocyanide Silicate
Glue-tannic acid	p	p	p	p	p	p
$Ni_3(CoCy_6)_2$	p	p	p	p	p	i
Ni_2FeCy_6	p	p	p	p	p	i
$Co_3(CoCy_6)_2$	p	p	p	p	i	i
Co_2FeCy_6	p	p	p (i)	i	i	i
$Cd_3(CoCy_6)_2$	p	i	i (p)	i	i	i
Nickel silicate	.	.	i	i	i	i
Cobalt silicate	.	.	i	i	i	i
$Cu_3(CoCy_6)_2$	i	i	i	i	i	i
Zn_2FeCy_6	i	i	i	i	i	i
Cu_2FeCy_6	i	i	i	i	i	i

In Table XIV are given Walden's results as regards the permeability of precipitation membranes to a number of positive ions bound (generally) to halogens.

The significant fact to be noted from Walden's results is that these membranes form a perfectly regular series in regard to their permeability to the substances examined, glue-tannic acid being the most permeable, and allowing the passage of everything investigated except alkali tannates and halides of (?) cadium, zinc and manganese, while copper ferrocyanide is the least permeable, the other membranes being intermediate in their permeability.

From these results and those obtained with a large number of acids, Walden concluded that the penetrability of substances depends not so much on the number and weight of the atoms composing their molecules, as on the nature and arrangement of the constituent atoms. Thus sulphate and thiosulphate have the same number of atoms in the molecule, but precipitation membranes are much more permeable to the latter than to the former. The same is the case with sodium acetate and sodium oxalate. In general, while both electrolytes and non-electrolytes may be able to pass through a membrane, acids and salts containing at least one univalent ion diffuse through most easily. Potassium and ammonium chlorides, bromides and iodides pass through membranes with nearly equal ease. With other

TABLE XIV

Permeability of Various Precipitation Membranes to Positive Ions bound (in most cases) to Halogens. (Data from Walden)

Membrane	Permeable to	Impermeable to
Glue-tannic acid	Alkalies, Cu, Ba, Mg, Fe″, Ni, Co, Hg″, Pb, Al	?Cd, Zn, Mn″
Ni_2FeCy_6	Alkalies, Mg, Ba, As	Ni, Co, Cu, Zn, Cd, Mn
$Ni_3(CoCy_6)_2$	Alkalies, Ba, As, Sb	Ni, Co, Cu, Zn, Cd, Mn
$Co_3(CoCy_6)_2$	Alkalies, Ba, Sb	Fe, Ni, Co, Cu, Zn, Cd
$Cd_3(CoCy_6)_2$	Alkalies, Ba, Sb	Cd, Co, Ni, Zn, Cu, Mn
Co_2FeCy_6	Alkalies	Mg, Ca, Sr, Ba (slightly permeable), As, Co, Ni, Cu, Zn, Cd, Mn
$Cu_3(CoCy_6)_2$	Alkalies	Fe, As, Ca, Ba, Zn, Cu, Co, Ni, Mn, Cd
Zn_2FeCy_6	Li, Na, K, Tl, NH_4, $C_2H_5NH_3$, $(C_2H_5)_2NH_2$ (slightly permeable)	Ca, Mg, As, Zn, Cu, Mn, Co, Ni, Cd, $(C_2H_5)_3NH$
Cu_2FeCy_6	Li, Na, K, Tl, NH_4	Be, Mg, Cu, Sr, Ba, As

bases the diffusion of halides is greater the greater the atomic weight of the base.

The effect on permeability of the addition of neutral salts to acids varies according to the acid. In some cases such addition is without effect (for example with hydrochloric and trichloracetic acids), in other cases there results a small hindrance to diffusion (as with sulphuric acid), while in other cases the addition of salts has a very significant effect (as with tartaric, glyceric and acrylic acids).

Tammann's observations on the penetration of 17 different dyes, including salts of colour bases, sodium salts of sulphonic acids, and acids, through three precipitation membranes, namely, glue-tannic acid, zinc ferrocyanide and copper ferrocyanide, showed seven exceptions to the regularity of the general order of permeability. Thus of the 17 dyes examined, eleven passed through the glue-tannic acid membrane, seven through the zinc ferrocyanide membrane and five through the copper ferrocyanide membrane. Nevertheless, fuchsin chloride, for instance, was able to penetrate the glue-tannic acid membrane and the copper ferrocyanide membrane, but not the zinc ferrocyanide membrane, although in general the zinc ferrocyanide membrane is more permeable than the membrane of copper ferrocyanide. An inverse case is that of cotton blue, to which the membrane of zinc ferrocyanide is permeable, but which can penetrate neither the copper ferrocyanide membrane nor the glue-tannic acid membrane, which is, in general, the most permeable of the three membranes examined.

It is to be noted in regard to the case of the permeability of the copper ferrocyanide membrane to fuchsin chloride, that according to Meerburg (1893) the dye is only able to penetrate the membrane until the latter is completely impregnated with dye.

Membranes then differ among themselves in regard to their permeability, and the permeability of any particular membrane is different to different substances. Generally the order of permeability to different substances is the same in the case of different membranes but there are exceptions to this rule. It would appear that membranes are much more permeable to halides than to sulphates and also considerably more permeable to salts of monovalent metals than to those of divalent metals. In some cases the permeability depends on the degree of dissociation of the substance but this is not by any means a universal rule.

Ostwald (1890) pointed out that in the case of a dissociated salt the membrane need only be impermeable to one ion of a salt in order to prevent both ions from passing, for on account of the electrostatic attraction of the oppositely charged ions the permeable ion will only travel to such a distance that its tendency to diffuse balances the electrostatic attraction.

It will be observed that very little quantitative work has been done on the permeability of membranes, and consequently exact data as to the influence of temperature and other factors on permeability are for the most part wanting. The influence of pressure on the passage of water through membranes has however been the subject of investigation by several workers, *e.g.* Schmidt (1856), Pfeffer (1877), Sebor (1904), Bigelow (1907) and Bartell (1911), from whose observations, and especially from those of Bigelow and Bartell, it appears that the rate of passage of water through membranes is proportional to the pressure. The membranes investigated by these different authors include various animal membranes (Schmidt), membranes of collodion and parchment paper (Bigelow), porcelain (Bigelow, Bartell), and copper ferrocyanide (Pfeffer, Sebor, Bartell).

The influence of temperature on the permeability of membranes of collodion to water at constant pressure was investigated by Bigelow and his results extended to porcelain by Bartell. The conclusion of these investigators is that the permeability expressed as the quantity of water passing through unit area of membrane in unit time, is given by the relation $M_\theta = M_0\,(1 + 0{\cdot}033680\theta + 0{\cdot}000221\theta^2)$, where M_θ, M_0 are the permeabilities of the membrane at temperatures $\theta°$, $0°$ respectively. As this formula is that connecting the viscosity of liquids at different temperatures the authors conclude that the

change in permeability of a membrane at different temperatures is nothing more nor less than a measure of the change of viscosity of the liquid.

There remain to be considered the various theories put forward to explain the differential permeability of membranes. There are two well-defined theories which are usually described as the sieve theory and the solution theory.

The sieve theory was first put forward by Traube (1867) who attempted to explain the semi-permeability of his precipitation membranes by supposing them to act as "atom-sieves" (more properly "molecule-sieves"), so that molecules below a certain size pass through, while those above this limiting size are kept back.

The experiments of Tammann and Walden already cited, as well as those of Kahlenberg (1906), do not wholly favour the sieve theory. Nevertheless, the theory has found in recent years a considerable number of supporters, *e.g.* Sutherland (1897), Perrin (1900). In an investigation on the passage of dyes through parchment paper Biltz (1910) found that the rate of passage of dye through the membrane depended very definitely on the dimensions of the molecule of dye. Thus when the number of atoms in the molecule did not exceed 45 the dye passed readily through the membrane; as the number of atoms in the molecule increases from 45 to 70 the rate of penetration through the membrane is slower and slower, and when the number of atoms in the dye molecule is greater than 70, the membrane is impermeable to the dye.

Also Bayliss (1915) points out that the difficulties in the way of the theory presented by Tammann's experiments in which the order of penetration of different substances varies with the membrane, can to a large extent be explained away.

Contrasted with the sieve theory is the solution theory of permeability, which may be traced back to the writings of Liebig (1849) and L'Hermite (1855). According to this theory substances pass through the membrane if they are soluble in the membrane, and are held back if they are insoluble in it. L'Hermite illustrated the theory with the "three liquid layers" experiments, one of which may be quoted as an example. Layers of water, castor-oil and alcohol were superposed in a cylinder, the castor-oil thus forming the layer separating water and alcohol. The alcohol is soluble in the castor-oil and passed through the middle layer composed of it (equivalent to a membrane) into the water. Similar experiments were performed with other systems of three liquids. The application of these experiments to the permeability of membranes

is obvious, and the solution theory of permeability has found many supporters, *e.g.* Nernst (1890), Kahlenberg (1906), and Overton (1897), to whose work more detailed reference will be made later.

From his work on the influence of pressure and temperature on permeability, Bigelow (1907) concludes that the passage of water through membranes of collodion obeys Poiseuille's formula for the movement of water through capillary tubes, and consequently that the passage of substances through such membranes is capillary in nature. The inconsistent results first obtained with porcelain were shown by Bartell (1911) to be due to mechanical clogging of the pores, a phenomenon which M. Traube thought he had been able to bring about in the case of precipitation membranes and which he adduced as evidence in support of the sieve theory. By clogging the pores of a membrane, the latter may become impermeable to substances to which it was formerly permeable. It has been pointed out by Bayliss (1915) that such clogging can also take place as a result of adsorption. The views of Bigelow seem at first sight to approach the sieve theory, but Bigelow shows that the capillary theory reconciles the opposed sieve and solution theories. In the case of porcelain the passage of water undoubtedly takes place through capillary pores, while in the case of water diffusing through collodion there is good evidence that the water passes through intermolecular spaces, *i.e.* dissolves in the membrane. But the phenomenon is essentially the same in the case of these and other membranes. Consequently Bigelow concludes that the rate of passage of liquids through molecular interstices is expressible by the same laws which formulate the rate of passage of liquids through capillary tubes.

This view, that capillary phenomena only differ in degree but not in kind, from chemical phenomena, can be traced back to L'Hermite.

Apart from the two definite theories of permeability here discussed, there has been suggested a third theory, which may be spoken of as the chemical theory, according to which the membrane is supposed to combine chemically with the substance to which it is permeable. This reaction is supposed to be reversible so that on the far side of the membrane the compound of membrane and diffusing substance breaks down with the result that the diffusing substance is set free on the far side of the membrane. This theory has been applied chiefly to cell problems, but has not found the support accorded to the sieve and solution theories.

(*To be continued*)

A STUDY OF SOME OF THE FACTORS CONTROLLING THE PERIODICITY OF FRESHWATER ALGÆ IN NATURE

By WILLIAM J. HODGETTS, M.Sc.

(With 6 figures in the text)

VII. *SPIROGYRA*

No less than 14 species of *Spirogyra* (namely *S. inflata, protecta* (= *calospora*), *colligata*[1], *longata, nitida, catenæformis, Grevilleana, condensata, maxima, bellis, varians, Jurgensii, mirabilis, Weberi*) have been observed in the pond during the period of observation, but although a few are hardy forms the majority are "spring annuals" (to use Transeau's term), and occur only during April—June, and are very rare or absent at other times.

As already stated (Section VI), *Spirogyra* predominates in the shallow-water marginal province, and rarely occurred in quantity in the central part of the pond during spring (February—May), culminating in a maximum generally in May, and rapidly declining in June, at the end of which month all species disappear, or become very rare, after producing zygospores. In the autumn (October—November) *Spirogyra* may again develop and become locally common in the pond, but is never so abundant as in the spring. The vernal phase was present in each of the four years, and was especially well developed in May 1919, when twelve species were observed, while an autumnal phase was present in 1918 and 1920, but was absent in 1919 (see below). The species which have appeared and conjugated in the autumnal phase are *S. inflata, protecta, colligata* and *varians*[2]. The pronounced development of *Spirogyra* during the spring (March—May) has been noted by many observers (14, 16, 17, 18, 30, 31, etc.), and the less-marked autumnal phase has been recorded by Fritsch and Rich (14, 16, 17), Delf (12), as well as others.

The frequency-curves of *S. inflata, S. protecta* and *S. colligata* are given in Fig. 4. Of these three species the first two are the hardiest

[1] Hawkesley Hall pond is the original locality where this interesting species (see Hodgetts, 20) was found.

[2] Fritsch and Rich (17) give *S. varians* as an example of a species which "appears to be quite confined to the vernal phase." Conjugating specimens of *S. varians*, however, have been collected during the autumn months from several other ponds near Birmingham.

of all the species of the genus noted in the pond, *S. inflata* more particularly tending to be a perennial form. It will be seen that the general trend of the curves for *S. inflata* and *S. protecta* are the same; for instance, the maximum in October 1918 carries over both species through the winter into the following vernal phase, and a similar behaviour is shown by *S. colligata* in the very mild winter 1920–1921.

There is little doubt that the vernal maximum of *Spirogyra* (as Fritsch and Rich (16) concluded) is the result of the periodic recurrence of a group of certain factors, of which temperature is undoubtedly important. All the species (except *S. bellis*) of the genus noted in the pond appear to flourish best when the monthly mean temperature falls between 6° and 12° C., although the hardier species are able to tolerate much lower temperatures—for example, *S. protecta* was observed in January 1919 in a state of conjugation under a cover of ice 3–5 cm. thick. The higher summer temperatures are distinctly unfavourable, except perhaps in the case of *S. bellis*, which occurred locally during June—August, 1919, when the mean temperature of the air was 14° to 17° C. The autumnal maximum always falls when the temperature-conditions again become favourable, but of course some other condition may play the part of a limiting factor and prevent the development of this phase (cf. case of autumn 1919, discussed below).

Sunshine is another important factor, and a comparison of the curves of Fig. 4 with the sunshine-data (Fig. 2) is interesting. The sunniest month in each of the three complete years was May, and this is the month in which *Spirogyra* was at its best each year. In the very sunny month May 1919 all the species of the genus recorded for the pond (except *S. bellis* and *S. Grevilleana*) were present and produced zygospores; and of these *S. inflata, nitida, protecta, mirabilis, longata, colligata* and also *Grevilleana* were again present (and in conjugation) in May 1920; while in 1921 the vernal phase was fairly well developed (*S. colligata, protecta, inflata, mirabilis* again conjugating) and reached a maximum in the very sunny May of that year. The relation to sunshine is most obvious in the case of the more sensitive species (*S. catenæformis, condensata, Jurgensii, mirabilis, longata, maxima, Weberi*) which were confined to the vernal phase (maximum in May); while in the case of the hardier species (*S. inflata, S. protecta,* and in a lesser degree *S. colligata* and *S. varians*), as an examination of the curves shows, the relation is much less obvious. Thus the autumnal phase of *S. inflata* and *S. protecta* in 1918 was at a maximum in a dull month (October) although growth was most marked in the fairly sunny September; and in

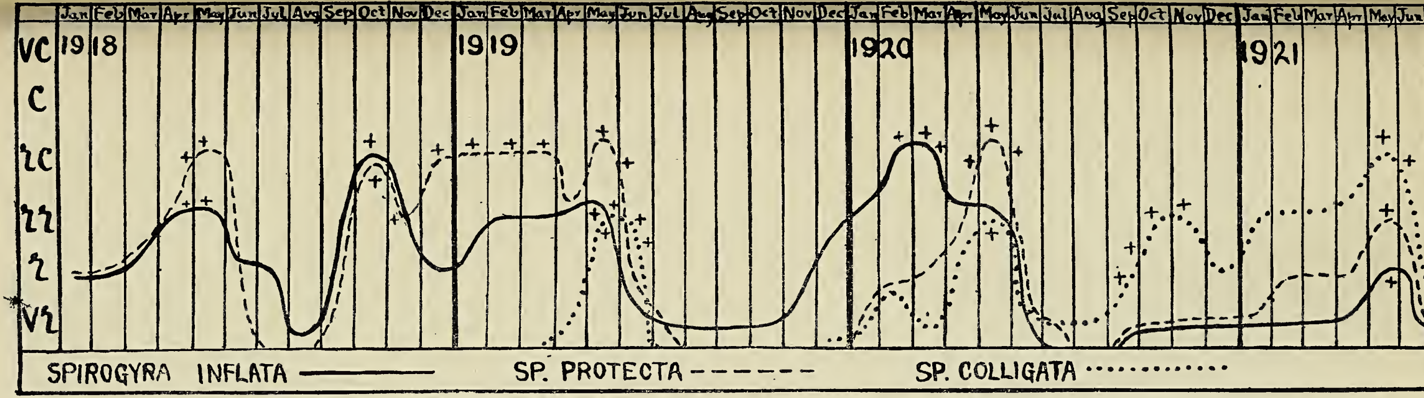


Fig. 4. Frequency-curves of three species of *Spirogyra*; vr = very rare, r = rare, rr = rather rare, rc = rather common, c = common, vc = very common; + denotes zygospore-production.

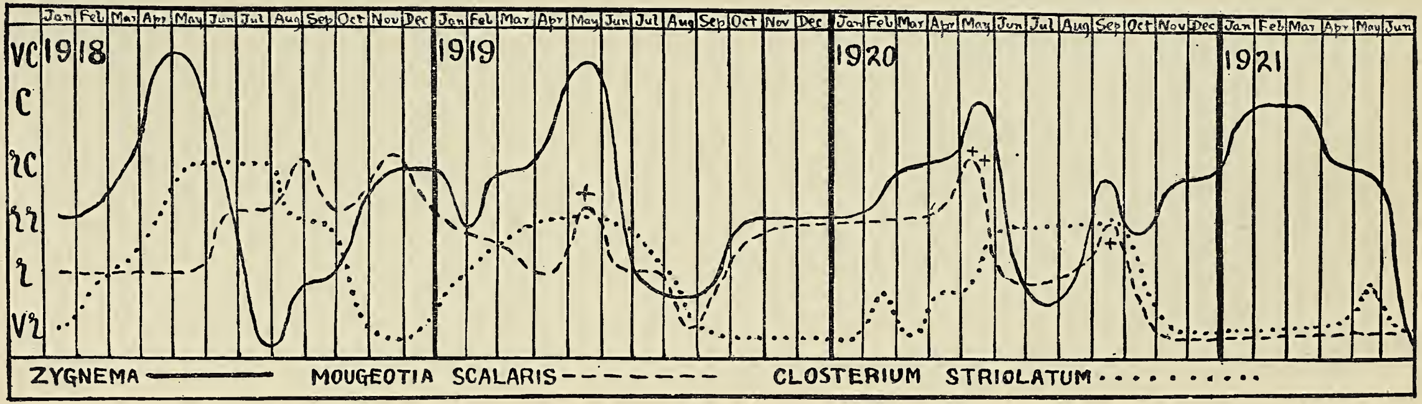


Fig. 5. Frequency-curves of *Zygnema* sp., *Mougeotia scalaris*, and *Closterium striolatum*.

1920 *S. inflata* reached its maximum and conjugated earlier than the other species, namely in February, and there was not much bright sunshine during January—February 1920.

An obvious relation is shown between the growth of *Spirogyra* in the pond and the amount of dissolved matter in the water (lowest curve Fig. 3). The greatest development of this genus coincided with a moderately low concentration of the water of 12 to 18 degrees, and undoubtedly this is the concentration which is most favourable, at any rate for the more sensitive species of *Spirogyra* (except perhaps *S. bellis*). During the spring of 1918 the concentration of the water was not determined, but in the autumn the concentration rose from 12 (September 21st) to 18 degrees (November 16th), and this corresponded to a pronounced autumnal phase in October (cf. Figs. 3 and 4). During the very pronounced *Spirogyra* maximum of May 1919 the concentration rose from 15 (May 17th) to 18 degrees (May 28th), but the further increase in the concentration during June resulted in the genus becoming rare.

An explanation is now forthcoming of the absence of an autumnal development of *Spirogyra* in 1919. During the summer of this year the water-level fell very low (see Fig. 3), and a very high concentration (reaching 30 degrees on November 22nd) resulted in the autumn, and there is every reason to believe that this was the particular factor which prevented the development of the genus during this season, especially as the meteorological conditions were favourable at that time. *S. inflata* is rather more tolerant in the matter of concentration (and also temperature and sunshine) than the rest of the species noted; the February maximum of 1920, for example, falling when the concentration was about 20 degrees, while the pronounced dilution of the pond during February—April 1920 affected this species but little (Fig. 4); and again in the early part of 1919 a similar disregard of a low concentration is shown by *S. inflata*, and also the hardy *S. protecta*.

The concentration-conditions during May 1920 were rather unfavourable, since after a fall to the very low concentration of 8 degrees on April 10th, and 9 degrees on May 8th, there was a very sudden increase to 18 degrees on May 29th[1]. Now of the six species of *Spirogyra* present during April—May 1920 (the most abundant being *S. longata, protecta, colligata* and *inflata*), by the end of May two (*nitida, mirabilis*) had disappeared, two (*protecta, inflata*) had become very rare, while *S. longata* and *S. colligata* each remained "rather rare." It thus appears that a sudden increase in the con-

[1] See p. 159 for explanation of this sudden increase.

centration is distinctly unfavourable towards at any rate the more sensitive species of *Spirogyra*.

Fritsch and Rich (16, 17) were led to suggest that the normally recurring vernal phase of *Spirogyra* was dependent among other conditions upon the realisation of a certain degree of concentration of the water, and although they reached this conclusion mainly from a consideration of the rainfall-data alone nevertheless their conclusion has been amply verified in the case of Hawkesley Hall pond.

It is obvious that the different species of *Spirogyra* are not all alike in the way they react towards external conditions. In the case of the present pond the hardiest species observed is *S. inflata*, which tended to be almost perennial, and, as already stated, is more tolerant in the matter of concentration, temperature and bright sunshine than all the others noted; while *S. protecta* is also hardy but rather less so than *S. inflata*. These two species are also those which appeared first and developed best in the autumnal phase of *Spirogyra* (when this was present) and which often persisted in some quantity throughout the winter. A rather less tolerant species is *S. colligata*, which appeared in the autumnal phase of 1920, while *S. varians* (present and conjugated in September 1920, as well as in May 1919, and the spring of 1912) probably comes near *S. colligata* as regards its degree of sensitiveness. The position of *S. nitida* (present in autumn of 1918, but not conjugating) is rather doubtful, but it does not appear to be a very sensitive species.

Very sensitive species which developed only in the vernal phases (March—May) are *S. catenæformis, Grevilleana, condensata, Jurgensii, mirabilis, longata, maxima* and *Weberi*[1]. These prefer a mean monthly temperature between 6° and 12° C., abundant bright sunshine and a moderately low concentration (between 12 and 18 degrees in the present pond) of the water. *S. bellis* developed rather exceptionally in the pond, but was confined to one small area, during June—August 1919, when the mean temperature was about 14°–17° C., and the concentration rising between 20 and 26 degrees, conditions which would undoubtedly preclude the growth of the majority of the species of the genus.

Pevalek (24) in his recent paper on the Algæ of N. Croatia found that the species of *Spirogyra* which appeared first in the annual cycle were the narrower ones with a single chloroplast and replicate endwalls, while in summer the wider species with several chloroplasts

[1] Doubtless these species might occur and even conjugate in the autumn if conditions were very favourable; Fritsch and Rich (17) noted *S. Weberi* in Abbot's pond in September 1905.

and plane end-walls developed, the order of appearance in the autumn being just the reverse[1]. This, as is obvious from the work of others, is a fairly general rule, and appears to be correlated with the fact, pointed out by Fritsch (15), that the species of *Spirogyra* present in the tropics are mostly broad forms with two or more chloroplasts and plane end-walls. Transeau (28) has analysed this annual succession of species of *Spirogyra* in more detail.

Of course many other factors besides those treated of above influence the growth of Algæ in a pond, and one which is undoubtedly important at times is competition between the various species present. In the case of the present pond during May 1919, when at least twelve species of *Spirogyra* developed in the comparatively narrow zone of shallow water at the side of the pond, two of these (*S. protecta, S. longata*) were "rather common," six were "rather rare," one (*S. condensata*) was "rare," and the remaining three (*S. Jurgensii, mirabilis, Weberi*) "very rare." Mutual competition between these various species was, in this case, the particular factor which determined the extent of development of each.

VIII. *ZYGNEMA* AND *MOUGEOTIA*

A species of *Zygnema* (width of filaments 22–24μ) is a perennial constituent of the algal flora of Hawkesley Hall pond, and, as mentioned in Section VI, is the dominant filamentous Alga in the central province of the pond during the spring, its maximum occurring usually at the end of April or in early May, although in 1921 the maximum fell exceptionally early (see curve in Fig. 5). The species was never observed to conjugate, and thus was not identified. Like *Spirogyra* it very rapidly decreased in amount towards the end of May, and was generally "rather rare" or "rare" by June. During the unfavourable summer-period it is rare and represented by more or less isolated and generally very short filaments, the cells of which, although comparatively thin-walled, are filled with abundant starch-grains, the whole contents of the cell being very dense, with an opaque granular appearance[2]. Growth again becomes apparent in September, while during the autumn and winter the Alga is often "rather common" (1918, 1920); and the very mild winter 1920–1921

[1] Pevalek explains this by reference to the intensity of the light, but this factor alone does not appear to supply a satisfactory explanation.

[2] These short cell-rows with the cells densely packed with food-reserves are sometimes termed "cysts" (see West (30), p. 34).

resulted in the maximum of 1921 falling very early (January—March)[1].

This species of *Zygnema* is much more hardy than even the hardiest species of *Spirogyra*. It became really abundant only when the temperature was moderate (a monthly mean temperature between 5° and 12° C.). The falling off of the species which usually commences in May (April in 1921) is due apparently to the combined influence of several factors, of which the increased temperature and competition with *Œdogonium* (see below, Section X) appear to be most active. The higher summer temperatures are particularly unfavourable, while the lower ones of winter may be tolerated: for instance in the winter 1919–1920 this Alga was "rather rare," while in that of 1918–1919 it was "rather common," apparently as a result of the mild November—December of 1918.

There seems little relation between the growth of *Zygnema* and the sunshine-data (cf. Figs. 2 and 5), unless it is that abundant bright sunshine is harmful. The pronounced development during March—April, and in October 1918, during April 1919 and 1920, and again in January 1921, in every case coincided with a rather dull or even a very dull month. The decrease in each of three complete years commenced in May (the sunniest month), so that excessive insolation may be a harmful factor, but it is difficult to separate its influence from that of the rising temperature.

A comparison with the concentration-curve in Fig. 3 shows that the most pronounced growth of this *Zygnema* coincides with low and moderately low concentrations of the water between 10 and 17 degrees, although it is clear that the form is very tolerant of other concentrations, both lower and higher. The conditions requisite for this species to conjugate were apparently not realised in the pond during the period of observation; or it may be that the species is one which conjugates very rarely, relying upon the production of "cysts" for tiding over unfavourable periods.

Filaments of *Mougeotia*, although almost always present in the pond, are generally rather scarce and more or less isolated. Two species (*M. scalaris* and *M. viridis*) have conjugated during the period of observation, but possibly other species have been present in a purely vegetative state in addition to these. The most abundant species of the genus in the pond was *M. scalaris*, a form which tends

[1] West (30) observes that the maximum growth of *Zygnema* in the upland lakes of the British Isles "usually occurs in the late summer and early autumn as the temperature is gradually declining." This obviously is not applicable to the species now under consideration.

to be perennial, and the frequency-curve of which is given in Fig. 5. Five "maxima" of varying intensity are shown (three autumnal and two vernal), namely in August and November 1918, May 1919 and 1920, and September 1920, the species in all cases growing mainly in shallow water towards the margin of the pond.

Delf (12) observed that a wide *Mougeotia* (probably *M. scalaris*), in ponds on Hampstead Heath, showed an autumnal as well as a vernal phase; while the sterile species noted by Fritsch and Rich (17) in Abbot's pool also exhibited an autumnal development in certain years, but tended to have its maxima during December—February.

M. scalaris in Hawkesley Hall pond is a hardy form as regards its ability to withstand extremes of temperature, the five maxima occurring respectively at the following mean temperatures: 16·5°, 5·5°, 13·5°, 12° and 13·5° C. (monthly mean temperatures of the air). A comparison with the data given in Fig. 2 shows that the species does not require any considerable amount of bright sunshine for good vegetative growth, but that abundant bright sunshine and a moderately high temperature (monthly mean between 11° and 13·5° C.) are requisite for zygospore-formation. In May of both 1919 and 1920 there were slight maxima, and the species conjugated, and this month in both years was very sunny (Fig. 2). Zygospores were very scarce in the feeble maximum of September 1920 (a dull month); and the larger maxima of August and November 1918 (the former a rather sunny and the latter a dull month) were purely vegetative, the sunshine of August 1918 apparently not being sufficient to induce conjugation.

There is distinctive evidence, therefore, that the conditions favouring vegetative growth, and those best for the conjugation of *M. scalaris* are not identical; and further instances of the same phenomenon will be noted in the case of the Desmidiaceæ (Section IX). Fritsch and Rich (18) have pointed out the connection between bright sunshine and the fruiting of *Mougeotia parvula*, as well as other Algæ, thus confirming Klebs' conclusion by direct observation in nature. It is certain, however, that many Desmids (see Section IX), as well as some species of *Spirogyra*, can conjugate without the stimulus of abundant bright sunshine.

With regard to the influence of the concentration of the water on the growth of *M. scalaris*, the evidence does not seem to point to any particular degree of concentration being essential for growth, in fact the species is a very hardy one in the matter of concentration of the water. Thus between November 1919 and April 1920, when the concentration fell steadily from 30 to 8 degrees (see Fig. 3), the

species remained "rather rare" the whole time. Competition with other filamentous Conjugates (particularly *Spirogyra* spp.), which tend to grow mixed with *Mougeotia* in the shallow-water marginal region of the pond, is undoubtedly a potent factor in determining the extent of development of *M. scalaris* at certain times of the year.

Narrow filaments of *Mougeotia* were also generally present in the pond, but mostly only rare or isolated. Of these narrower forms *M. viridis* became "rather common" at the sides of the pond, and produced a fair number of zygospores, during September and October 1920, but declined during the following winter, and was not again observed. This slight autumnal development of *M. viridis* is interesting since, in this country, it is more particularly an early spring Alga. West (30) has pointed out that in the British Isles *M. viridis* is almost invariably the first species of the genus to fructify in spring—in the Midlands and Southern counties in March with a water-temperature of 5°–7° C. (*l.c.* p. 33). In the present pond it developed when the temperature was falling and the monthly mean (air-temperature) was between 13·5 and 10·5° C., and when the concentration was falling from 18 to 12 degrees, and the sunshine poor. The evidence is incomplete but it seems as though abundant bright sunshine, so essential for zygospore-production in the case of *M. scalaris*, can to a considerable extent be dispensed with by *M. viridis*; in which case an interesting parallel can be drawn between *Mougeotia* and *Spirogyra*, since the narrower species of the latter genus (*e.g. S. inflata*) require in a lesser degree the stimulus of bright sunshine in order to conjugate than do the wider species (cf. Section VII).

IX. THE DESMIDIACEÆ

Desmids are present in Hawkesley Hall pond all the year round, and are represented by a rather large number of species (see Section V). The following have been most abundant, and are those whose periodicities have been most thoroughly worked out: *Hyalotheca dissiliens, Sphærozosma granulatum, Closterium acerosum*[1], *Cl. striolatum, Cl. moniliferum, Cl. Kützingii, Cl. lineatum*[1], *Pleurotænium Ehrenbergianum, Cosmarium Botrytis*[1], *C. Regnellii, Staurastrum brevispinum*[1], *S. Dickiei*[1], *S. furcigerum, Xanthidium antilopæum, Arthrodesmus convergens.* Many of these tend to be scattered throughout the pond, although showing a preference for the deeper water, amongst the filaments of *Œdogonium, Zygnema*, etc., but a

[1] These have produced zygospores.

few (*e.g. Closterium acerosum*) prefer the shallower water at the sides of the pond.

As regards their occurrence in the pond these Desmids may, for convenience, be divided broadly into two groups, the majority, however, falling in the second group.

GROUP I contains those Desmids which attain their maximum either in the spring or autumn (or have two maxima, one in spring and another in autumn). To this group belong *Hyalotheca dissiliens*, *Sphærozosma granulatum* and *Closterium acerosum* (Fig. 6).

GROUP 2 includes those Desmids which attain their maximum development at the end of summer or in early autumn (June—September), and includes all those of the list, with the exception of the three placed in the first group. *Closterium striolatum*, however, rather tends to form a connecting-link between these two groups.

From a consideration of the meteorological and other data it seems certain that the most important factors concerned in the development of all the Desmids of the pond are temperature and the concentration of the water. It is found by a comparison of the various curves that pronounced development of any particular Desmid depends on the conjunction of certain average temperature-conditions with a more or less definite concentration of the water, and that if only one of these conditions is favourable then the unfavourable one plays the part of a limiting factor and prevents the increased growth of the species.

Hyalotheca dissiliens (Fig. 6) is the hardiest of all the Desmids present, and a perennial constituent of the algal flora of the pond. It tolerates considerable extremes of concentrations (as in latter half of 1919, and first half of 1920), but nevertheless became more or less abundant only when the concentrations were moderately low (between 10 and 18 degrees—as during October—November 1918, April—May 1920, August—September 1920).

Again this species can withstand considerable variations in the temperature-conditions although distinctly preferring the moderate temperatures of spring and autumn; while the most unfavourable time for this Desmid, during the period of observation, was the hot summer of 1918. The lower temperatures of winter affect this Desmid in a much less marked degree than do the higher summer-temperatures. No relation to bright sunshine is apparent. The absence of a distinct vernal phase in 1920 was probably due to the marked dilution which the pond underwent during February—April of this year, favourable concentration-conditions apparently not arising until the higher unfavourable temperatures had set in—in short, the

low concentration of water possibly acted as a limiting factor during the early part of 1920.

Sphærozosma granulatum (Fig. 6) is a form decidedly more sensitive than *Hyalotheca*, as regards concentration of the water, but it may withstand somewhat higher temperatures, a monthly mean temperature between 6° and 13° C. apparently being most favourable. Higher summer-temperatures appear to have been harmful in 1918, but less so in 1919. The greatest observed development (October 1918) fell with the concentration rising gradually from 12 to 18 degrees, while the increase of this species during April—May 1919 also took place when the concentration was rising approximately between 10 and 18 degrees. The high concentrations attained in the latter half of 1919, and the sudden variations in the concentration during April—May 1920 (see Fig. 3), were much more unfavourable for this Desmid than they were for *Hyalotheca*, and caused the slight maximum of 1920 to fall late in the year, namely during August—October. It may be noted that the temperature-conditions during the cool summer of 1920 were never very unfavourable towards this species. No explanation can be offered for the non-appearance of *Sphærozosma* in the spring of 1921. There seems no relation to sunshine unless it is that continued bright sunshine is harmful (May 1918 and 1919), but it is difficult to separate the influence of this factor from that of the higher temperature.

Closterium acerosum (Fig. 6), in contrast to almost all the other Desmids of the pond, tends to thrive best in very shallow water at the margin of the pond. It is a typical vernal Desmid, although in 1918 it showed two maxima, one in spring and another during September—October. Vegetative growth was most active with a monthly mean temperature (of the air) between 7° and 13° C. (either falling or rising), and when the concentration of the water was between 10 and 16 degrees. During the autumn of 1919 the temperature was favourable (see Fig. 2), but the high concentration (cf. Fig. 3) was a limiting factor which prevented growth; and again the moderately high concentrations which prevailed during the dry spring of 1921, were doubtless the cause of the "maximum" of that season being very slight—in fact only in one month (April) did the concentration fall to a favourable degree, and this is the month in which the "maximum" occurred.

With reference to the conjugation of this species (which occurred in May 1919 and 1920), it is obvious that bright sunshine is a very important factor in bringing this about. During the maximum of October 1918, a month poor in sunshine, no conjugation was

observed—conditions were favourable only for vegetative growth; but in May 1919 and also 1920, both months with very abundant sunshine (cf. Fig. 2), zygospores of this species were locally common. A certain amount of vegetative growth generally precedes zygospore-production in all the Conjugates, and in April 1918 and 1921 this requisite degree of development in the case of the present species apparently was not attained. *Cl. acerosum*, in requiring abundant bright sunshine for conjugation, agrees with certain other Conjugates which have produced zygospores in the present pond (cf. *Spirogyra* spp., *Mougeotia scalaris*, *Cosmarium Botrytis*), although, as will be shown below, certain Desmids of the pond conjugated without the stimulus of bright sunshine.

Closterium striolatum (Fig. 5), as already mentioned, rather tends to form a connecting-link between the two broad groups into which the Desmids of the pond have been divided. The maximum of *Cl. striolatum* tends to fall when the average temperature-conditions fall between 7° and 14·5° C. (usually in spring and early summer, but throughout the whole of the mild summer of 1920), while the most favourable concentrations of the water lie between 12 and 20 degrees. Thus the species is adapted to rather higher temperatures, and distinctly higher concentrations than *Cl. acerosum*, although it can hardly be termed a summer-species. High temperature was probably the cause of the decrease of this Desmid during July—August 1918 (since the concentration remained favourable), but the decline during June—July 1919 was probably due more to the high concentration of the water than the temperature. The long-continued maximum of 1920 (up to September) was due to the fact that *both* temperature and concentration remained favourable during the cool summer of this year (cf. Figs. 2 and 3).

The Desmids of the second group—those whose development is favoured by the higher temperatures of summer and early autumn—now come under consideration. The periodicity-curves of three of these are given in Fig. 7. *Cosmarium Botrytis* (Fig. 7) shows a comparatively regular curve the maximum heights of which fall generally between May and September. The relation to the temperature (cf. Fig. 2) is obvious, monthly mean temperatures between 10° and 15·5° C. being necessary for good development. There is also a distinct relation to the concentration-curve (Fig. 3), the most favourable concentrations lying between 15 and 20 degrees. The rather early decline of this species towards the end of July 1919, at a time when temperature-conditions remained favourable, was obviously due to the high concentration of the water (rising to 27

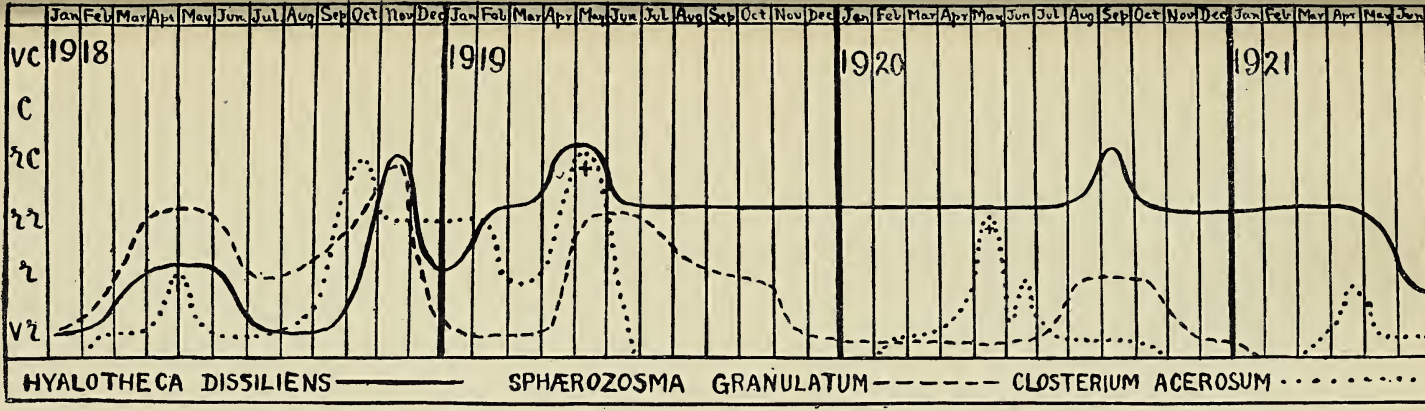


Fig. 6. Periodicities of three of the Desmids of Hawkesley Hall pond.

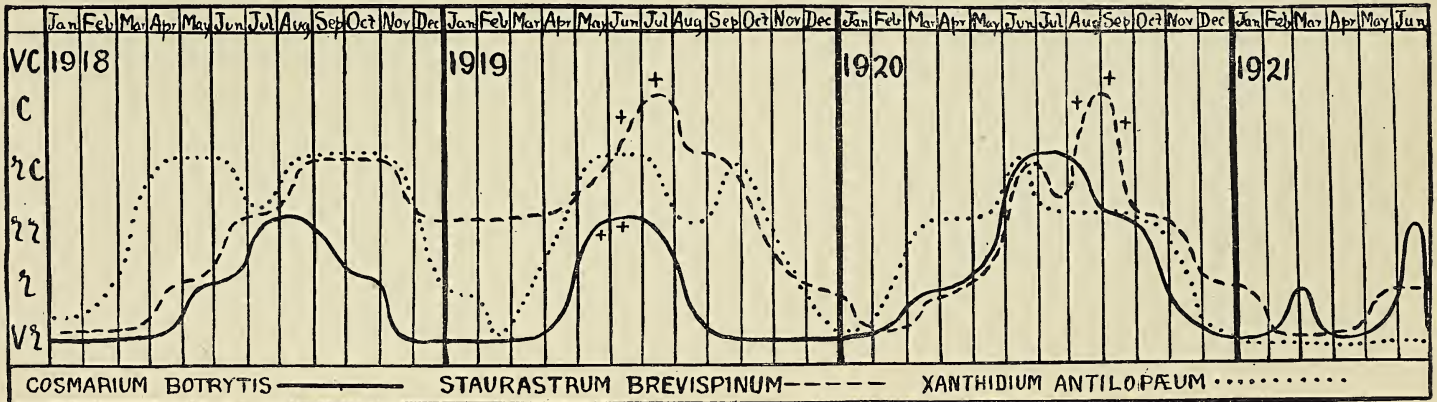


Fig. 7. Periodicities of three of the Desmids (summer-forms) of Hawkesley Hall pond.

degrees on August 22nd, 1919); and the decrease at the end of June 1921 was doubtless due to the same cause.

From a consideration of the sunshine-data it appears that only moderate amounts of bright sunshine are sufficient for good vegetative development, but that abundant bright sunshine is essential for conjugation. Zygospores were observed (locally common) during May and early June 1919, and May 1919 was a record month for sunshine (Fig. 2). It is true that in 1918 the species attained its maximum in a sunny month (July), and no zygospores were observed in that year; perhaps they may have been scarce and were overlooked. It is probable, therefore, that this Desmid agrees with *Closterium acerosum*, *Mongeotia scalaris*, *Spirogyra* spp., and doubtless many other Conjugates, in requiring abundant bright sunshine for zygospore-production.

Cosmarium Regnellii gave a frequency-curve of almost exactly the same form as that of *C. Botrytis*, but was never represented by so many individuals as the latter species. *Cosmarium reniforme* was frequently observed in the samples from the pond but was generally very rare, although it showed a slight increase during the warmer months of the year.

Staurastrum brevispinum was one of the commonest Desmids observed in the pond, and gave a frequency-curve (in Fig. 7) the maxima of which tend to fall rather later than those of *Cos. Botrytis*, namely some time between July and early September, when the monthly mean temperature was between 13° and 16·5° C. The species, however, tends to persist in some quantity into the middle (1919) or even to the end (1918) of autumn, while it remained "rather rare" during the winter 1918–1919. It is thus a fairly hardy form, but attains its best development under summer-conditions. The most favourable degree of concentration of the water appears to lie between 14 and 21 degrees, and while lower ones are tolerated the higher concentrations apparently acted adversely in August and again in October 1919 (cf. with data in Fig. 3). There seems no relation between bright sunshine and vegetative growth.

Zygospores[1] of this species were observed in the pond during June—July 1919, and again in August--September 1920, and, rather contrary to what might have been expected (cf. *Closterium acerosum* and *Cosmarium Botrytis* above), there seems little relation between bright sunshine and zygospore-production in this Desmid. The 1920

[1] Apparently never recorded before since W. and G. S. West in their *Monograph of the British Desmidiaceæ* state (4, p. 146) that the zygospores of this Desmid are unknown. They are 50–53μ diam., and have a thick, smooth, colourless wall.

maximum, especially, occurred after a month (July) poor in sunshine (cf. Fig. 2), yet zygospores were noted at the time to be "locally rather abundant," It is true that conjugation took place during the maximum of 1919 after two months of very sunny weather (cf. data in Fig. 2), but on that occasion zygospores were recorded as "very rare." The evidence therefore points to abundant bright sunshine not being essential for the conjugation of this species. It is interesting to note that West (30) was led to conclude that the precise conditions resulting in zygospore-formation in Desmids "are probably widely different for various species" (*l.c.* p. 35); and the present observations rather tend to confirm this view.

Two other species of *Staurastrum* (*S. Dickiei*, *S. furcigerum*) were present in the pond, but since their frequency-curves tend to follow very closely that of *S. brevispinum* they have not been reproduced here. Both tend to arrive at a maximum towards the end of summer, persisting as "rather common" until the middle of autumn, when they always decrease and remain "rare" (or "very rare") during the winter and early spring. All three species of *Staurastrum* were very tolerant of the high concentration (27 degrees) attained in August 1919, and all three remained "rather common" during August and September of that year. In this respect they are distinctly more hardy than the species of *Cosmarium* in the pond. This is quite the reverse of the conclusion arrived at by Fritsch and Rich (18) in the case of the Desmids of Barton's pond, since these authors concluded that the two species of *Staurastrum* (*S. tricorne*, *S. brevispinum*) were apparently much more sensitive to high concentrations of the water than the *Cosmarium* spp. and *Closterium* spp. present in that pond.

Zygospores of *Staurastrum Dickiei* were observed in the pond, but were scarce, on one occasion only, namely on August 7th, 1920 (when *S. brevispinum* was also in conjugation), and this was after a rather dull July, so that *S. Dickiei* appears to agree with the very closely allied *S. brevispinum* in not requiring abundant bright sunshine for conjugation to take place.

Xanthidium antilopæum (Fig. 7) is a perennial constituent of the algal flora of the pond, and is more abundant in the warmer months. A monthly mean temperature between 10° and 15·5° C. is essential for this species to become really common, although it may persist as "rather rare" at temperatures rather lower than these. The low temperatures of winter are decidedly harmful. The relation to the concentration of the water is again obvious (cf. Figs. 3 and 7), the most favourable concentration lying between 14 and 20 degrees. An

example of a high concentration causing a depression in the frequency-curve is apparent in July and August 1919; but the fall in the concentration during September 1919 caused the frequency-curve to rise again, although the further increased concentration (and also the falling temperature) during October soon caused the Alga to decline once more.

The following table gives the frequencies of the three remaining Desmids which were of importance in the pond.

Table[1] showing the Occurrence of Three of the Desmids present in Hawkesley Hall Pond during 1918–1921.

		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Pleurotænium Ehrenbergii	1918	vr	vr	r	r	r	rr	rc	rc	rc	r	rr	rc
	1919	rr	rr	rr	rr	rr	rr	r	vr	vr	vr	vr	vr
	1920	vr	r	r	r	r	rr	rr	rr	rc	rr	rr	r
	1921	r	r	r	r	r	rr						
Closterium moniliferum	1918	vr	r	rr	rr	rr	rr	rr	rc	rc	rr	rr	rr
	1919	rr	rr	rr	r	rr	rr	r	r	vr	vr	vr	vr
	1920	vr	vr	vr	vr	r	rr	r	rr	rr	r	r	r
	1921	r	vr	r	r	r	r						
Closterium lineatum	1918	vr	vr	vr	vr	vr	r	rr	vr	vr	vr	vr	r
	1919	vr	vr	vr	r	r	rr	vr	vr	vr	r	vr	vr
	1920	vr	vr	vr	vr	vr	r	r	r	rr !	r	vr	vr
	1921	vr	vr	vr	vr	vr	vr						

All three it will be noted tend to have their maximum development during the summer or early autumn. Temperature seems to be the main determining factor, although sunshine may, in a lesser degree, be important. In general concentrations of the water between 14 and 20 degrees are most favourable; and, as with most of the other Desmids, the high concentrations attained in the second half of 1919 proved harmful. The curious secondary maximum of *Pleurotænium* in December 1918 was probably due to the fact that this month was abnormally mild (see Fig. 2). Both species of *Closterium* given in the table prefer distinctly higher temperatures than *Cl. acerosum*, the occurrence of which has already been discussed, although *Cl. moniliferum* (like *Cl. acerosum*) persisted as "rather rare" throughout the winter of 1918–1919.

The curious double zygospores of *Cl. lineatum* were observed in the pond (but were scarce) in early September 1920, and since

[1] The meaning of the symbols in this and in subsequent tables, and in the figures, is as follows: vr = very rare, r = rare, rr = rather rare, rc = rather common, c = common, vc = very common, – = absent; + (in the figures) and ! (in the tables) indicate sexual reproduction.

August 1920 had only a moderate amount of bright sunshine it seems that this species rather tends to follow *Staurastrum brevispinum* and *S. Dickiei* in not requiring abundant sunlight for conjugation, while differing in this respect (as in the matter of temperature) from *Cl. acerosum*. The same applies to *Cl. rostratum*, which was occasionally seen in the pond, although always very rare, the zygospores of which were observed in April 1919, a month which had only a moderate amount of bright sunshine. The Desmids of the pond which have conjugated thus fall into two classes, (1) those which require abundant bright sunshine before conjugation can take place (*Closterium acerosum, Cosmarium Botrytis*), and (2) those which apparently are able to conjugate given only a moderate amount of sunshine (*Staurastrum brevispinum, S. Dickiei, Closterium lineatum, Cl. rostratum*). The evidence in the case of the two species of *Closterium* in the second class, however, is not quite conclusive, since these Desmids were never present in any quantity.

X. THE ŒDOGONIACEÆ

Species of *Œdogonium* are always present in Hawkesley Hall pond, and as regards their periodicity can be sharply separated into two groups.

Group 1 contains probably only one species of *Œdogonium*, a wide species (width veg. fil. 30–35μ), which since it has never reproduced sexually during the period of observation cannot be named, but which nevertheless is the most important of all the species of the genus observed in the pond, and is the form referred to simply as *Œdogonium* in the account (in Section VI) of the annual cycle observed in the central region of the pond. As already mentioned this species attains a huge maximum in the central deeper water of the pond generally during June—August, large masses of its filaments during these months occupying sometimes all the available free water-surface between the floating leaves of *Potamogeton natans* (cf. Section II).

Group 2 includes the rest of the species of *Œdogonium* occurring in the pond, and which even when taken all together were never as abundant as the species of the first group, and were never more than moderately wide (up to 20μ wide). Their maximum growth was always attained during May or early June, a rapid decline taking place in the latter month after oospore-production. This group includes *O. cryptoporum, O. crispum, O. Borisianum, O. Braunii, O. echinospermum* and *O. rugulosum*. Several species of this group rather tended to show a preference for the shallower water at the

sides of the pond, often occurring in quantity round the submerged parts of rushes, etc., but *O. cryptoporum* and *O. Braunii* were also at times rather abundant in deeper water.

Dealing first with the wide species of the first group, the frequency-curve of which is given in Fig. 8, there is obviously a marked relation shown towards temperature (cf. Fig. 2), since the various maxima always coincide with the higher temperatures (a monthly mean between 12° and 16·5° C.), while the decline after a maximum is simultaneous with the lowering of the temperature at the end of summer or in early autumn. There was an exceptional smaller secondary maximum in the very mild October of 1920; while the maximum was attained very early (April) in 1921, probably owing to the warm spring of this year. There seems little or no relation towards bright sunshine, although growth was most marked in very sunny months in 1918 and 1920, yet in 1919 pronounced growth took place during March—April and again in July, and both these periods were poor in sunshine (cf. Fig. 2); and again the marked increase of the species in the abnormally mild January of 1921 was due solely to the rather favourable temperature, since this month was very dull.

An important factor affecting the vernal increase of this form is competition with *Zygnema* in the central parts of the pond. It has already been stated (Section VI) that the wide species of *Œdogonium* replaces the *Zygnema* usually during June, so that competition between these two genera must be most marked in May and June; and it may be that this competition with *Zygnema* tends to prevent the species of *Œdogonium* now under consideration from attaining its maximum early in the year, as do the narrower species of the genus in this pond. Although the *Zygnema* is a vernal type while the wide *Œdogonium* is a summer-form, yet during the transition from spring to summer there is every reason to believe that there is active competition between the two, since both occupy identical positions in the pond, and the latter is not large enough for both to attain any great maximum at the same time.

A comparison of the frequency-curves of *Zygnema* (in Fig. 5) and the wide *Œdogonium* (in Fig. 8) rather bears this out. In the first place the rise in the *Œdogonium*-curve, just before a maximum, generally involves a fall in the *Zygnema*-curve; and further, in 1918 and 1919 at the periods of maximum development of the *Zygnema* the upward tendency of the *Œdogonium*-curve is interrupted by a horizontal portion—a form of curve which indicates that some limiting factor has come into play, and is checking further growth. That this particular limiting factor is competition with the *Zygnema*

is indicated by the fact that upon its removal by the sudden decrease of *Zygnema* (usually in early June) the *Œdogonium*-curve again ascends to a higher level. In this connection the behaviour of the two curves in early 1921 is interesting. Owing to the very mild January of 1921 both Algæ succeeded in becoming "common" by the end of that month, but mutual competition checked further increase until the end of March (shown by the flattening of both curves during January—March), when the *Œdogonium* assumed the upper hand and became "very common" during April, and, apparently as a consequence, the *Zygnema* suddenly decreased in amount.

Little relation is shown between the concentration of the water and the growth of this wide species of *Œdogonium*, although active development generally took place with moderately strong concentrations between 16 and 20 degrees (1918, 1920); but in 1919 the Alga was "very common" in August when the concentration was as high as 27 degrees (cf. Fig. 3).

Of the narrower species of *Œdogonium* (of Group 2) probably the most abundant was *O. cryptoporum*, the frequency-curve of which is also given in Fig. 8. The curves for the other species of this group, enumerated at the beginning of this section, are practically identical in form with that of *O. cryptoporum*, although the height of the May—June maximum varies with the different species (the result, doubtless, of mutual competition), the least abundant species being *O. Borisianum*, *O. Braunii*, and *O. rugulosum*. The spring-maximum (end of May and first half of June) was observed in each of the four years, and occurred with the average temperature of the air rising between 10° and 13·5° C., while the decline towards the end of June, after fruiting, coincided with the setting in of summer conditions. These species of the genus thus prefer a distinctly lower temperature than the wide species already considered.

The relation to the sunshine-data (Fig. 2) is very marked, the maximum always falling after a spell of very sunny weather. This agrees with the observations of Fritsch and Rich (18) who found that the maximum development of the species of *Œdogonium* in Barton's pond was "determined by the first month with plenty of bright sunshine." The second conclusion of these authors regarding these species, namely that "dilute water is more favourable to their development than concentrated water" (*l.c.* p. 78), is hardly confirmed by the present observations. The maximum of the species of *Œdogonium* which have fruited in Hawkesley Hall pond always occurred with medium concentrations between 16 and 20 degrees (cf. Figs. 3 and 8); and it may be noted that a sudden increase in

the concentration, as during May 1920 when the concentration rose from 9 to 18 degrees in the course of the month (cf. Fig. 3), did not check the development of these species.

It will be noticed that in regard to the species of the genus which were identified there is no evidence that the conditions requisite for good vegetative growth differ in any way from those essential for oospore-production, although, of course, such a difference may possibly exist. Undoubtedly the most curious feature about the occurrence of *Œdogonium* in the pond was the independent way in which the wide sterile species continued its great maximum after the almost complete disappearance (during June) of the narrower species which had fruited. It may be that the wide species, having become perennial in the pond, has dispensed with sexual reproduction, or only resorts to it very occasionally.

The genus *Bulbochæte* is rather scantily represented in the pond, but *B. minor* has been observed during the spring of each of the four years, and although never abundant its frequency (Fig. 8) may be briefly referred to. Its maximum development fell usually during April—May (April—July in 1919), and it is undoubtedly a vernal form preferring average temperatures between 8° and 13° C., thus resembling very closely the species of *Œdogonium* which fruited in the pond. The latter species have doubtless been partly responsible for the feeble development of *Bulbochæte* in the pond, since both generally grow together upon the same substratum (submerged stems of rushes, etc.) and are thus in competition with each other. In this connection it is noteworthy that *Bulbochæte* (mainly *B. minor*, but *B. intermedia* was also noted) was rather better developed in April—May 1918, as compared with the other years, and the narrower species of *Œdogonium* were poorly represented during the spring of 1918. The dependence of *Bulbochæte* on abundant bright sunshine is very obvious (cf. with sunshine-data in Fig. 2), and this condition is very probably essential for the sexual reproduction of this genus.

XI. *TRIBONEMA*

This genus is represented in Hawkesley Hall pond by *T. bombycinum* (the type, and also its forma *minor*) and *T. affine*. As already stated in Section VI *Tribonema* is most abundant in shallow water near the sides of the pond during late autumn and winter, when it is often the best-developed filamentous Alga in the pond, although during the colder months *Spirogyra* (see Section VII) may be locally common, and *Microspora* (Section XII) may be more or less developed in places.

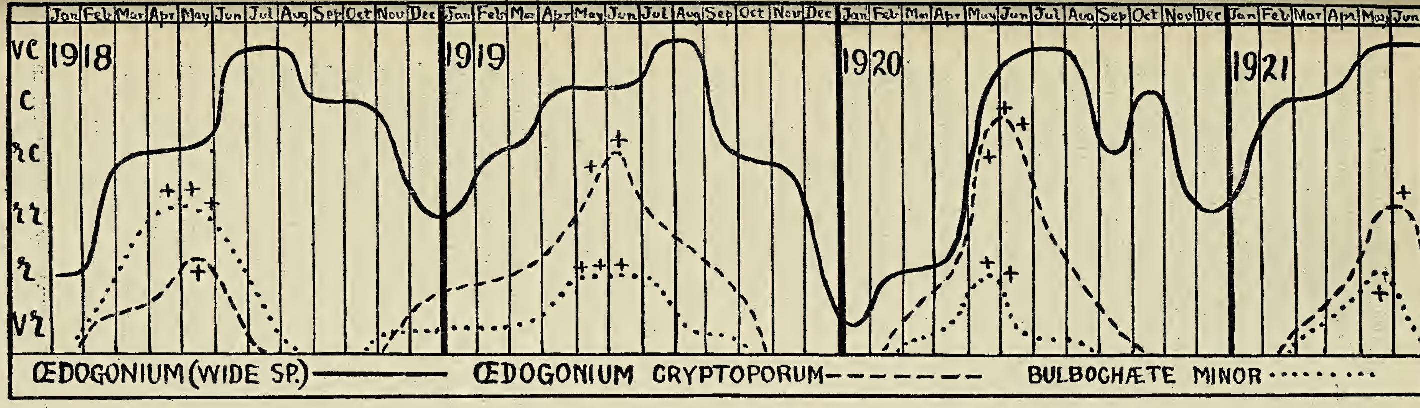


Fig. 8. Frequency-curves of three members of the Œdogoniaceæ in Hawkesley Hall pond.

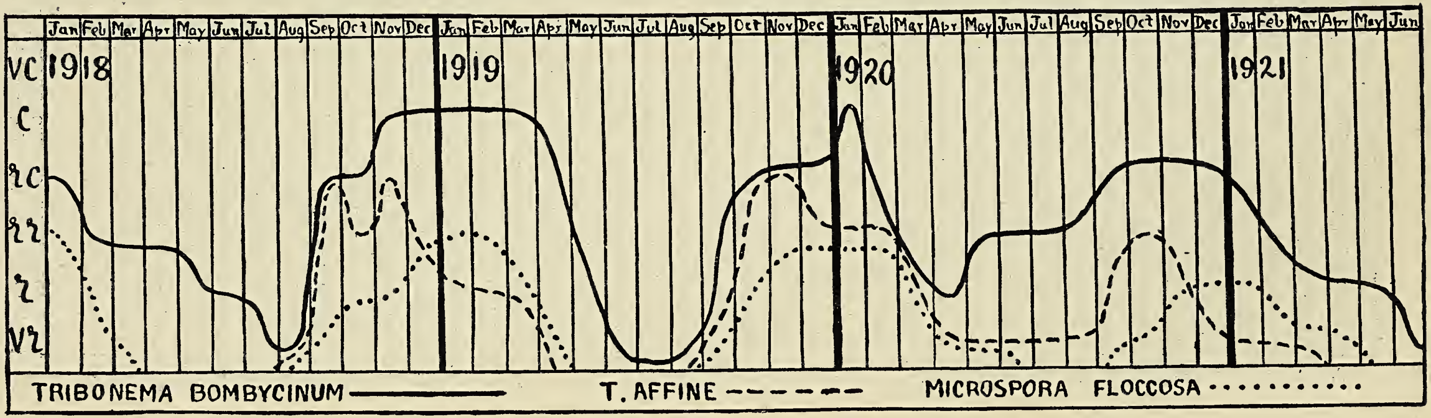


Fig. 9. Frequency-curves of *Tribonema* (two species) and *Microspora floccosa*.

The periodicity of *T. bombycinum* (type), given in Fig. 9, is represented by a fairly regular curve. Development commenced during September in 1918 and 1919, and the species rapidly reached a maximum which lasted throughout the following winter, the decline setting in usually in early spring (end of March in 1919, and January—February in 1921), while during the warmer months the Alga is usually rare[1]. The species flourishes either when the temperature is falling (autumn), or when it remains persistently low or rather low; while the rising temperature of spring seems very unfavourable. A marked feature of its frequency-curve is the fact that during the notoriously cold summer of 1920 the species persisted as "rather rare," whereas it was "very rare" in the hottest months of the two preceding summers.

A marked antagonism appears to exist between the growth of *T. bombycinum* and bright sunshine (cf. data in Fig. 2), the maxima of the frequency-curve of this species always occurring when the daily mean of bright sunshine during the month is less than three hours; although, as with many other species, it is difficult to separate the influence of sunshine and high temperature. The adverse influence of bright sunshine on the development of several members of the Heterokontæ was emphasised by Fritsch and Rich (18), and the present observations tend to confirm this in the case of *Tribonema*. It was noted that the species of this genus showed a preference for those parts of the margin of the pond which were most shaded by the leaves of grasses, and the various marginal Phanerogams.

There seems almost no relation between the concentration of the water and the growth of *T. bombycinum*, low, moderate, or even very high (October—November 1919) concentrations apparently all being the same to this species. The very high concentrations towards the end of 1919 (see Fig. 3) apparently depressed its frequency-curve only to a slight extent. Some explanation seems necessary to account for the early decline of the species in late January and during February 1920, at a time when temperature-conditions remained favourable (see Fig. 2). February 1920 was somewhat sunnier than usual, but hardly sufficiently so to account for the observed decline, and a probable adverse factor was the sudden fall in the concentration of the water during February—March 1920 (Fig. 3), although the evidence is not quite conclusive. *T. bombycinum* was always observed to form abundant aplanospores towards the close of each of its periods of abundance (during February—April 1919, March

[1] No indication of two phases, such as were shown by this species in Barton's pool (18), was observed in the present pond.

1920, February 1921.) Generally two rounded aplanospores were formed in each cell and the filaments broke up into H-shaped pieces in order to set them free. In addition to forming these aplanospores, however, the species generally persisted through unfavourable periods by means of isolated vegetative filaments.

T. bombycinum f. minor was quite as frequent in the pond as the type form, and its periodicity was worked out separately, but since the resulting curve is almost identical with that of the type (given in Fig. 9) it has not been reproduced here. Undoubtedly this form is influenced by external conditions exactly in the same way as the type, and the two were generally found intermixed, so that the above remarks concerning *T. bombycinum* apply with equal force to its forma *minor*. Doubtless between such closely allied forms growing together competition must be very active. No aplanospores were ever observed in the case of *T. bombycinum f. minor*, the Alga always tiding over unfavourable seasons by means of isolated filaments.

T. affine was in general decidedly less abundant that *T. bombycinum*, with which it was usually mixed. Its frequency in the pond (given in Fig. 9) very closely resembles that of *T. bombycinum*, activity commencing during the falling temperature of early autumn, and a maximum reached in October or November. Other factors, apart from temperature, however, caused the behaviour of this species to vary somewhat during the winter months, the most important probably being the concentration of the water. While *T. affine* apparently agrees closely with *T. bombycinum* in the matter of temperature and also sunshine, it reacts somewhat differently in regard to the concentration of the water. On two occasions (November 1918 and 1919) the position of the maximum on the *T. affine* curve coincides with the highest concentration reached during the autumn and winter months (cf. data in Fig. 3), and on one of these occasions (November 1919) the concentration was the highest (30 degrees) observed during the period of observation. In *T. affine*, therefore, we have an Alga which has its period of development (autumn—winter) determined mainly by the low temperature and scarcity of bright sunshine, although the actual position of maximum growth in this period is conditioned by the concentration of the water, the "maximum" coinciding with the highest concentration attained during the season.

There seems little doubt from the above observations that *T. affine* is able to utilise directly the organic peaty compounds which were abundant in the pond during times of high concentrations (cf.

Section IV), although culture experiments would perhaps be necessary to prove the matter definitely. Others have noted this preference of *T. affine* for peaty water: West for example (31) stated that *T. affine* "is not uncommon in peaty ponds and ditches" (*l.c.* p. 430). Doubtless the fact that this species has usually only two small, very pale chromatophores lends support to the view that its nutrition in nature is mixotrophic (cf. *Chlamydomonas*, Section XVII, and the Cyanophyceæ, Section XVIII).

There was doubtless a certain amount of competition between the two species of *Tribonema* in the pond, as a comparison of the curves suggests, and in the following section it will be seen that there was also fairly obvious competition between *Tribonema* and *Microspora*—genera showing very similar periodicities and usually found growing together in the shallow-water marginal region of the pond. Competition between these two genera was also noted by Fritsch and Rich (18) in Barton's pond.

XII. *MICROSPORA*

This genus was never very abundant in the pond, although represented by two species, *M. floccosa* and *M. stagnorum*, the former being the more important. From the frequency-curve of *M. floccosa*, given in Fig. 9, it will be seen that the maxima tend to fall regularly in the coldest months of the year, when the monthly mean temperature is between 1·5° and 5·5° C., and there is no doubt that a low temperature is the most important factor determining the occurrence of this species. This agrees with the observations of Fritsch and Rich (18) who found that the maximum development of *M. amœna* var. *gracilis* in Barton's pond was determined by the lowest winter-temperatures. The rather late attainment of the maximum of *M. floccosa* in 1918, as compared with 1919, is correlated with the fact that November and December 1918 were rather mild (cf. Fig. 2); while the general scarcity of the species in the winter 1920–1921 was doubtless due to this season being very mild.

As will be seen from Fig. 9, *Microspora* and *Tribonema* tend to arrive at a maximum at the same time of the year, and since the two generally grew together it is fairly obvious that the former genus suffered by competition with the latter. Exactly why *Tribonema* always succeeded in getting the upper hand, and operated as a limiting factor checking the growth of *Microspora*, it is difficult to say; the actual conditions favouring the last-named genus would have to be studied more fully in some pond where its development is not restrained by competition with other species. The case of *Micro-*

spora and *Tribonema* in this pond is somewhat analogous to that of *Bulbochæte* and *Œdogonium* (see Section X).

Certain filaments of *M. floccosa* always passed into the akinete-condition towards the close of the vegetative period (usually during March), persisting in this way throughout the summer months. *M. stagnorum* generally occurred mixed with *M. floccosa*, and like the latter is a cold-water species, although it is clear that it was affected very adversely by competition with *M. floccosa* and also *Tribonema*. It exhibited a slight maximum in October 1918 (mean temperature 9° C.), but the abundance of *Tribonema* (and *M. floccosa*) caused a quick decline in early November. A further maximum occurred in November—December 1919, the development of the species coinciding with that of *M. floccosa*. Both the latter species and *M. stagnorum* show no relation to the concentration of the water.

Here it may be noted that it seems a general rule that the occurrence of any Alga which is struggling to develop under conditions in which it is adversely influenced by competition with other species (of animals or plants) will tend to show little or no relation to such factors as concentration of the water and bright sunshine (although it may still exhibit some relation towards temperature), since it is *competition* which is the particular factor which sets a limit to the growth of the species, and restrains its development even though all other factors may be favourable for its increased growth. In small bodies of water, such as Hawkesley Hall pond, and with numerous species present, it is very probable that more or less competition is going on at all times of the year.

XIII. *VAUCHERIA*

This genus was represented in the pond by two species, *V. aversa* and *V. sessilis*, although the latter was present in quantity only upon one occasion. The occurrence of *V. aversa* is given in the following table:

Table[1] showing the Occurrence of *Vaucheria aversa* in Hawkesley Hall Pond during 1918–1920.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1918	—	—	—	—	—	—	—	r	rr	rr	r	c!
1919	rc!	rr!	rr!	vr!	vr	—	—	—	—	vr	vr	rr
1920	rc!	rc!	r!	vr	vr	—	—	—	—	—	—	—

[1] For symbols see footnote on p. 210. An exclamation mark denotes oöspore-production.

V. aversa tends to develop best in fairly shallow water near the sides of the pond, and generally forms more or less definite communities, often almost unmixed with other filamentous species, although sometimes growing in company with *Tribonema bombycinum*. It is a form which prefers cold or moderately cold water, the most favourable temperature apparently being a monthly mean between 4·5° and 8° C., and thus development tends to fall in autumn or winter, while the species may persist into the following spring (see table above). It was most abundant during late December 1918 and early January 1919, when the concentration of the water was rather low, namely 13 degrees (cf. Fig. 3); while a smaller maximum occurred during January—February 1920, with the concentration in the neighbourhood of 20 degrees. The evidence, although not conclusive, points to moderate or rather low concentrations being preferred. During the very high concentrations at the end of 1919 (Fig. 3) the species was very rare, and did not commence development until late December, when the concentration was falling very rapidly.

Bright sunshine is certainly not necessary either for good vegetative growth or for the development of sexual organs in *V. aversa*, since both the maxima coincided with periods very deficient in sunshine. *V. aversa* thus differs from many species of *Spirogyra* and *Œdogonium* (and apparently also from *V. repens*, according to the experimental work of Klebs) in fruiting without the stimulus of bright sunshine[1].

From the usual mode of occurrence of *Vaucheria* it appears that abundant aeration of the water is essential for good development, and this is borne out by the present observations on *V. aversa*, since the various maxima of this species always followed a month of heavy rainfall, when there would be a marked increase in the gaseous content of the water, since the rain of course would bring in a supply of dissolved gases from the atmosphere, and the prevailing low temperature would favour the continuance of this condition. The slight vegetative development of *V. aversa* which occurred during September—October 1918 (cf. above table) coincided with a phenomenally wet September (see rainfall-data in Fig. 3); while December 1918 was the second wettest month of the year, and the species again increased during that month. December 1919 was also the second wettest month of 1919 and *V. aversa* showed increased development during that month.

[1] Fruiting specimens of *V. aversa* (and *V. geminata*) have been collected on several occasions from small pools near Birmingham, and always in the colder months of the year when sunshine is deficient.

Vaucheria sessilis has been found in the pond on three occasions, namely October 1919 (rare), September 1920 (very rare), and April—May 1921 (rather rare) and was absent, or occasionally perhaps rare and vegetative only, at other times. Although the evidence is insufficient this species apparently differs in its requirements from *V. aversa*. During its period of greatest development in the pond (April—May 1921) the average temperature of the air was between 7° and 11° C., the concentration of the water was rising between 15 and 18 degrees, there was abundant sunshine, and rain was very deficient during the preceding three months, so that the aeration of the water was probably poor.

XIV. *APHANOCHÆTE* AND *DRAPARNALDIA*

Aphanochæte repens and *Draparnaldia glomerata*, although not very important constituents of the algal flora of the pond may be briefly referred to. The occurrence of the former species is given in the following table:

Table showing the Occurrence of *Aphanochæte repens* in Hawkesley Hall Pond during 1918–1921.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1918	vr	vr	r	r	rr	r	vr	vr	r	rr	rr	r
1919	r	rr	rr	rc	rr	rr	rr	vr	vr	vr	vr	vr
1920	vr	vr	vr	vr	rr	r	r	vr	vr	rr	rr	rr
1921	rc	rc	rc	rr	r	r						

Aphanochæte repens was observed in the pond as an epiphyte upon the wide sterile species of *Œdogonium* (rarely upon the narrower species, and very rarely upon *Microspora*) which generally formed such a conspicuous feature in the central parts of the pond during the summer months (cf. Section X and the curve of this species in Fig. 8). The occurrence of *Aphanochæte* it will be noted shows only a slight relation to the periodicity of its "host," since although the maximum development of the epiphyte occurred either in May (1918, 1920), April (1919), or during January—March (1921), which in each case coincided with the vernal increase of the species of *Œdogonium* in question, yet *Aphanochæte* always decreased in amount long before the *Œdogonium* commenced to decline. In fact *Aphanochæte* is a spring-form (although sometimes showing a certain amount of development in the autumn, as in 1918 and 1920), preferring moderate temperatures (a monthly mean between 4° and 11° C.). The higher temperatures of summer are very unfavourable

towards its growth. In the spring-like winter of 1920–1921 it will be noticed that the species reached its maximum very early (January 1921).

Aphanochæte prefers low or moderately low concentrations between 10 and 17 degrees; high or very high concentrations (as in second half of 1919) are particularly harmful. Of course the presence of a suitable "host" upon which to grow is essential for this species, but in Hawkesley Hall pond fortunately the wide species of *Œdogonium* was generally so abundant (except in the colder months) that lack of a suitable "host" was rarely a factor limiting the growth of this epiphyte[1]. But such a condition obtained in April 1920, in which year the wide *Œdogonium* commenced development much later than usual (see curve of this species in Fig. 8), and when it did commence rapid growth at the end of April and early May the *Aphanochæte* developed *pari passu* with it until the end of May, when the higher temperature stepped in and caused the epiphyte to decline.

Draparnaldia glomerata attained only one maximum in the pond during the period of observation, namely in January 1920 (it was "rather common"), when the mean temperature of the air was about 5° C., and the concentration of the water rather high (falling, and between 24 and 20 degrees). The species is undoubtedly a cold-water type, and tends to have its maximum development during the winter months, as noted by Delf (12), and also by the present author in the case of certain other ponds near Birmingham. Why it did not appear during the winter 1918–1919 cannot be decided from the data available; perhaps the prevailing low concentration of the water at that season had something to do with it, or perhaps the species was suppressed by severe competition. Its absence in the winter 1920–1921 was perhaps due to the very mild conditions which obtained during that season. During February 1920, towards the close of its period of development in the pond, the species produced abundant aplanospores.

XV. *NITELLA* AND *COLEOCHÆTE NITELLARUM*

Nitella flexilis was observed in Hawkesley Hall pond from 1919 to 1921, and it was always accompanied by *Coleochæte Nitellarum*, an endophytic species which grows between the lamellæ of the outer cell-walls of *Nitella* (and *Chara* spp.). The periodicities of these two species are given in the table below.

[1] Compare in this respect the relation between *Nitella* and *Coleochæte Nitellarum* in the pond, discussed in the next section.

Table showing the Occurrence of *Nitella flexilis* and *Coleochæte Nitellarum* in Hawkesley Hall Pond during 1919–1921.

		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nitella flexilis	1919	—	—	—	vr	r	rc!	rc!	rr!	rr!	rr	rr	vr
	1920	vr	vr	vr	rr!	rr!	r!	vr	vr	rr!	rc!	rc!	rc
	1921	rc	rc	rr	rr	vr	r						
Coleochæte Nitellarum	1919	—	—	—	vr	vr	rr!	rc!	rr!	rr!	r	vr	—
	1920	—	—	vr	r	rr!	r!	vr	—	r	r	r	rr
	1921	rr	rr	rr	r	vr	vr						

Nitella flexilis developed rather irregularly in the pond, and in the form of more or less local patches growing from the bottom in places where the water was only moderately deep. Its growth was undoubtedly greatly hindered by the extensive development of *Potamogeton natans* during the summer (cf. Section II), probably owing to the fact that the floating leaves of this plant cut off considerable light from the bottom of the pond; and it was observed that the patches of *Nitella* were always confined to those parts of the water where the floating leaves of *Potamogeton* happened to be poorly developed or absent altogether. No very close relation to the temperature is apparent; the first maximum occurred when the monthly mean temperature fell between 13·5° and 14·5° C., the second with a rising spring-temperature, while the rise to the third maximum coincided with a falling temperature in autumn, although the species persisted in quantity throughout the succeeding mild winter. Apparently a moderately high temperature (a monthly mean between 9° and 14° C.) is best for good vegetative growth, although somewhat lower ones are tolerated.

A rather close relation is shown between the vegetative growth of *Nitella* and the sunshine-data, while abundant bright sunshine is particularly essential for the development of sexual organs in this species. Thus the increase to the first maximum, in 1919, was preceded by two months of very sunny weather, while development towards the end of March 1920 coincided with a sunny March (see data in Fig. 2). Sexual organs were formed in abundance in the case of the maximum of 1919 and the first maximum of 1920, when the species had the stimulus of abundant sunshine (see Fig. 2), but were scarce during September—November 1920 (dull months), and absent altogether during the remaining months (which were dull, but mild) of this long-continued third maximum. There is no doubt therefore that oospore-production in *Nitella flexilis* is favoured by abundant bright sunshine.

No relation can be demonstrated between the concentration of the water and the growth of *Nitella*. The marked development during May—June 1919 coincided with a concentration rising from 18 to 20 degrees, but the high concentration (27 degrees) of August 1919 apparently affected this species very little, while the slight maximum during April—May 1920 occurred with an extremely low concentration (cf. Fig. 3).

With regard to the endophytic *Coleochæte Nitellarum* it will be noted at once on reference to the above table that the growth of the *Coleochæte* followed almost exactly that of the *Nitella*. This means that the amount of the latter plant present in the pond always operated as a limiting factor and restrained the growth of the endophyte, a condition of affairs just the reverse of that which obtained between *Aphanochæte* and the wide *Œdogonium*, discussed at some length in the last section. With the two last-named species it was noted that the epiphyte had a periodicity very different from that of its "host," and this might, or might not, have been the case with *Coleochæte Nitellarum* and *Nitella* had the latter plant been more abundant in the pond. Thus an epiphyte is unable to exhibit, so to speak, its true periodicity when its growth is held in check by the scarcity of a suitable "host," and under such conditions its occurrence will tend to follow very closely that of its "host," although this does not necessarily mean that the two are influenced in the same way by external conditions.

It may be pointed out that abundant bright sunshine is also essential for the development of oospores in *Coleochæte Nitellarum*. This is shown by the fact that in 1920, although development commenced in March, no oogonia were observed until the end of May (the first very sunny month); and further by the fact that no oogonia were observed in the case of the third maximum (September 1920—March 1921) which developed during a dull period.

XVI. THE PROTOCOCCALES

The principal members of this group which have been at all abundant in Hawkesley Hall pond are *Dictyosphærium Ehrenbergianum*, *Ankistrodesmus falcatus*, *Scenedesmus denticulatus* var. *linearis*, *Pediastrum Boryanum* and *P. tetras*. The first-named species was the most abundant, and its occurrence is given in Fig. 10, while the table below gives the periodicities of the remaining four species.

Table showing the Occurrence of Four Members of the Protococcales in Hawkesley Hall Pond during 1918–1921.

		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ankistrodesmus falcatus	1918	vr	vr	vr	r	rr	rc	rr	rr	r	vr	rr	r
	1919	r	vr	vr	vr	vr	vr	rr	rr	r	r	r	r
	1920	vr	vr	vr	vr	vr	vr	r	rr	rr	rr	vr	vr
	1921	vr	vr	vr	vr	r	r						
Scenedesmus denticulatus var. *linearis*	1918	vr	vr	vr	r	rr	rr	rc	rr	r	r	vr	vr
	1919	—	—	vr	vr	vr	vr	rr	rr	r	r	r	r
	1920	vr	vr	vr	vr	vr	r	rr	rc	rr	r	vr	vr
	1921	vr	vr	vr	vr	vr	vr						
Pediastrum Boryanum	1918	vr	vr	vr	vr	vr	vr	rr	rr	rr	rr	r	vr
	1919	vr	vr	vr	vr	vr	vr	vr	r	rr	r	vr	vr
	1920	vr	vr	vr	r	r	r	r	rr	rr	rr	r	r
	1921	vr	vr	vr	r	r	r						
Pediastrum tetras	1918	—	vr	vr	vr	r	r	rr	r	r	r	vr	vr
	1919	vr	vr	—	—	vr	vr	vr	r	r	r	vr	vr
	1920	vr	vr	vr	vr	vr	vr	r	r	rr	rr	vr	vr
	1921	vr	vr	vr	vr	vr	vr						

All these forms exhibit a fairly uniform periodicity, their development being most pronounced during the warmer months, the maximum generally occurring at the end of summer or in early autumn. In general moderately high temperatures are preferred[1], although it appears that with certain of the species the higher summer-temperatures are distinctly unfavourable[2]. The next most important factor is the concentration of the water, and in the present pond a moderately high concentration between 16 and 22 degrees appears to supply the best conditions as far as this factor is concerned (cf. however *Pediastrum* below). No relation to bright sunshine is apparent.

The aquatic animal life of the pond is another factor of importance influencing the development of these algal species, since, of course, many aquatic animals feed voraciously upon them. In Hawkesley Hall pond animal life was fairly well developed throughout the greater part of the year, although rather more abundant during spring and early summer; and this may have caused the various members of the Protococcales to attain their maximum development rather later in the year than they otherwise would have done.

[1] This agrees with the observations of West (31) who states that the great majority of the Tetrasporine and Chlorococcine Protococcales are late spring and summer forms, often occurring far into the autumn.

[2] Fritsch and Rich (18) found that *Sphærocystis Schrœteri* was adversely affected by high summer-temperatures in Barton's pond.

Dictyosphærium Ehrenbergianum (Fig. 10) is a perennial constituent of the algal flora of the pond, its maxima falling in the middle or towards the end of summer (June—July 1918, July—August 1919, August 1920). The most favourable temperature appears to be a monthly mean between 12° and 15° C. (cf. data in Fig. 2), and higher temperatures appear to be rather harmful, as shown by the decline of the species in July 1918, at a time when other conditions seemed favourable. From a comparison with the concentration-curve (in Fig. 3), it is apparent that gradually rising concentrations between 16 and 22 degrees are those most suitable for this species in the present pond, while a decreasing concentration—even between these limits—is distinctly unfavourable. The sudden decline of the species at the end of August 1919 (cf. Fig. 10) was due either to the high concentration of the water (27 degrees) attained in this month, or to the sudden decrease in the concentration during August—September, or again to the high temperature of August, or, more probably, was the result of more than one of these factors.

Ankistrodesmus falcatus[1] (cf. above table) is also adapted to moderately high temperatures (a monthly mean between 11° and 14° C.); and again higher temperatures apparently caused a decrease of the species in July 1918. In 1920, probably on account of the favourable temperature-conditions (see Fig. 2), the maximum persisted well into the autumn. The relation towards the concentration of the water is much the same as with the last species considered, the most favourable concentration for growth lying between 16 and 22 degrees, although the species may persist in fair quantity with concentrations outside these limits. A falling concentration does not appear to be so harmful to this species as it was with *Dictyosphærium*.

Scenedesmus denticulatus var. *linearis* closely followed *Dictyosphærium* in its occurrence, although it is a decidedly more sensitive form. A monthly mean temperature between 12·5° and 15·5° C. appears to supply the best temperature-conditions for growth; and again higher summer-temperatures were concerned in bringing about a decrease of the species (in August 1918, and perhaps August 1919) after the July maximum, although the concentration of the water probably also played a part. The species increased to a maximum generally when the concentration was rising and between 16 and 21 degrees. The slight lowering of the concentration during June—July 1920 (cf. Fig. 3) apparently did not have any adverse influence on

[1] The vars. *acicularis* and *spirilliformis* of this species showed a periodicity in the pond similar to that of the type, but they were always much less abundant than the latter

this Alga, but in each of the three complete years the decline after the maximum coincided exactly with a marked decrease in the concentration, a coincidence which can hardly be considered as accidental.

Pediastrum Boryanum and *P. tetras* are both favoured by the higher summer temperatures, a monthly mean temperature (of the air) between 13° and 16° C. being requisite for pronounced growth; and in no case did a high temperature ever influence these two species adversely. Little relation is shown by *Pediastrum* towards the concentration of the water. In the case of *P. Boryanum* the increase to the normal maximum may take place either when the concentration is very high (August 1919), or moderately high (June—July 1918 and July—August 1920); while the moderately low concentrations during September—October 1920 apparently affected neither species of this genus adversely, the decline at the end of October 1920 being due to the lowered temperature. Temperature thus appears to be far more important than concentration of the water in determining the development of *Pediastrum*.

In concluding this section it may be noted that these five members of the Protococcales, in regard to the temperatures most favourable for their development, form a sort of series, at one end of which is *Ankistrodesmus*, for which a monthly mean temperature of the air between 11° and 14° C. is most suitable and the higher temperatures unfavourable, while at the other extreme there are the two species of *Pediastrum*, adapted to the highest summer-temperatures, while the two remaining forms are intermediate as regards their behaviour towards temperature.

(*To be continued*)

A NEW METHOD OF VEGETATIVE MULTIPLICATION IN *CROTALARIA BURHIA*, HAM.

By R. H. DASTUR, M.Sc. and W. T. SAXTON, M.A.

(With Plate II and 1 figure in the text)

Introduction

While investigating some ecological problems on an area close to Ahmedabad, the writers made a preliminary investigation of the root structure of typical plants of the formation studied. That of *Crotalaria burhia* presented some peculiarities of sufficient interest to warrant a separate account. This species is perennial, while the other local species of *Crotalaria* are annuals.

External Examination

The root in the youngest plant[1] we have observed is a straight tap root about 4 ft. long, and in a plant of some years old, the tap root is estimated to be about 16 ft. in length. The actual length dug out on one occasion was 12 ft. but the entire root was not taken out. There are many lateral roots from deeper portions of the main root in younger plants but the development of dormant lateral roots takes place in the upper part also as the plant gets older. In a plant about a year old, the axis is seen to be ribbed, the ribs appearing first in the transition region from root to stem and extending downwards into the root where they gradually disappear. In old plants the ribs are thick and conspicuous (Plate II, fig. 1). They also anastomose with one another as they pass downwards.

A well grown plant reaches two to three feet in height and bears linear leaves $\frac{1}{2}$ in. by $\frac{3}{16}$ in. In a young plant there is only one unbranched shoot. Branches appear in succession all over the upper part of the main shoot. On the lower part close to the base of the main shoot other branches grow from buds, and as the plant gets older they all grow almost to the size of the main shoot and may give rise to secondary branches. The ribs already described end just above the base of the main shoot, extending also into the base of the

[1] Probably less than one year old.

lowest branches and completely surrounding them. The various branches described above we propose to distinguish by the word "normal."

After a long time the main shoot with the upper branches dies back to the point where the ribs surround it, and that portion of the main shoot increases in size owing to the ribs getting thicker and more prominent than before. Both these phenomena occur later in the case of the lower branches also.

Afterwards small buds appear terminating some of the ribs, earlier in the main shoot than in the lower normal branches. These give rise to new branches different in origin (as will appear later) from the "normal" branches and we propose to call them "reproductive" branches. These reproductive branches, which appear ribbed for a short distance from the base, give rise to secondary *reproductive* branches below and secondary *normal* branches above.

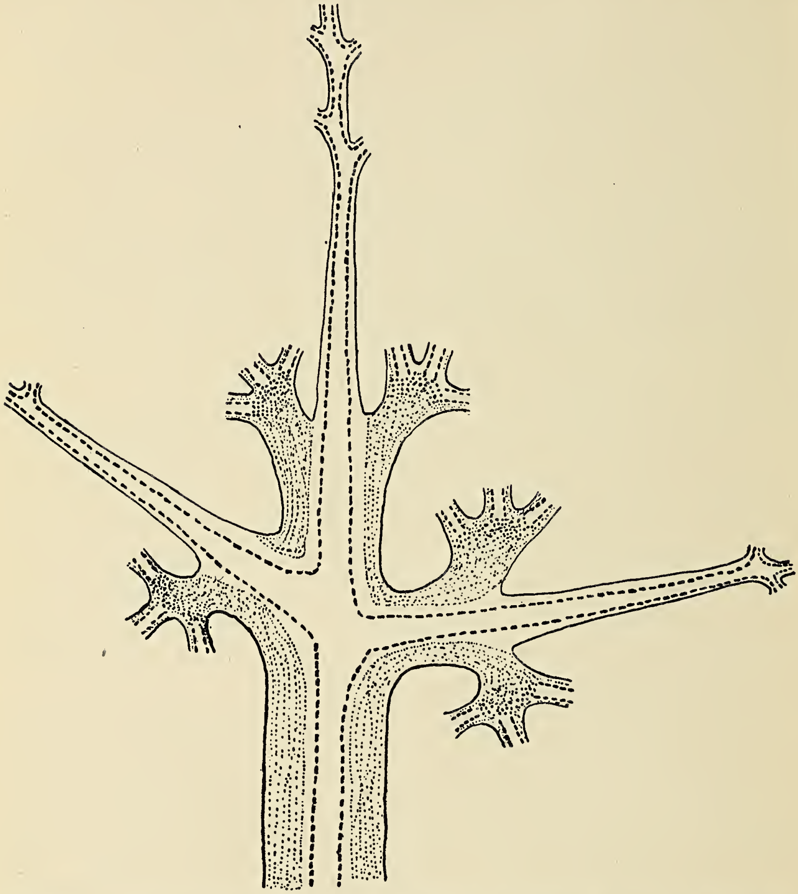
Internal Structure

A series of transverse sections of the root from the apex to the base was prepared and examined. There is a central cylinder in which secondary thickening takes place at a very early stage, so much so, that it is very difficult to identify the protoxylem in sections prepared only 6 ins. from the apex of the root. The marked feature of the secondary thickening is the great thickness of the phloem. On examining the sections it was clear that the ribbed appearance of the root and portions of the main shoot and branches already described was due to the formation of accessory bundles.

From the sections cut near the apex it was observed that the formation of the cork cambium takes place very early, in the cortex just outside the endodermis. The cells of the cortex are quite typical and differ in form from those of the pericycle in which cork cambium next appears, and the endodermis thus disappears. The cells just below the cork then become meristematic and the first xylem vessel of the accessory bundle appears. Such single xylem vessels appear almost simultaneously at five or six points near the periphery (fig. 2). It seems clear that they are formed in the pericycle. New xylem elements are added to each as well as some phloem, and small bundles are thus produced which project radially (fig. 3). Many such accessory bundles appear in succession, some of them in approximately radial rows. The later formed bundles are always either outside previously formed ones or at fresh points on the circumference (figs. 4 *a* and 4 *b*). Cork formation takes place around the various accessory bundles,

but for a time these remain connected. The cork formation also takes place between the central cylinder[1] and the accessory strands.

The vascular supply of the normal branches consists as usual of branches from the central cylinder of the main shoot. In this way



Text-fig. 1. Diagrammatic longitudinal section to show the way in which the accessory system gives rise to reproductive branches independently of the main central cylinder. The thick broken lines show the normal vascular tissue, the thin dotted lines the accessory bundles.

they are directly connected with the conducting tissues of the main root. The accessory bundles surround the lower part of the main

[1] The term "central cylinder" is here and hereafter used to denote the cylinder of primary vascular bundles, and not, obviously, in the more usual sense of all tissues within the endodermis.

shoot and the normal branches and those regions gain in thickness as the accessory bundles increase in number and grow older. The reproductive branches, which appear later in these lower regions of the main shoot and normal branches, arise directly from accessory bundles and have no connection with the central cylinder of the shoots on which they are borne, nor consequently with the main strands of the root (Text-fig. 1). The same remarks apply to secondary reproductive branches produced on the primary reproductive branches. Thus all these reproductive branches differ in origin from normal branches. But normal secondary branches which are also produced on these reproductive branches are directly connected to the central cylinder of the branches on which they arise. So in old plants, the original vegetative shoot and the normal branches do not exist, and all the shoots are connected only with the accessory bundle system. The central cylinder of the main root dies back from above, after the original shoot and normal branches are dead, and in old plants, a hollow tube of the accessory strands, with decayed matter inside, may be seen extending some distance below the ground. In old plants the accessory strands also separate into groups owing to the formation of cork, but they remain connected below. The groups of accessory strands, as has been seen, terminate in "reproductive" branches, and the latter are therefore carried further apart by the separation of the groups. The accessory system remains attached to the main root below, where the formation of cork has not taken place, and where the accessory bundles decrease in number and become less conspicuous, until, traced downwards, they disappear.

Much light was thrown on many points in this investigation by the preparation of a skeleton of the root, along with the lower portions of the main shoot and branches, by maceration. The skeleton was prepared by allowing it to decay in water for a fortnight and then keeping it in dilute nitric acid for a day. It was quite clear then that the reproductive branches arose directly from the accessory bundles and had no connection with the main central cylinder.

The accessory system in the root at first appeared to be entirely separate from the central cylinder, and it was thus difficult to see how it could function as a conducting system as it did not seem to develop in relation to any absorbtive tissue. It was found, however, from sections cut at points where lateral roots originated, that the conducting tissues of the lateral roots, though formed primarily as a branch of the central cylinder, were connected by a few strands with the accessory bundles. The central cylinder becomes functionless

as the main shoot and the normal branches die, and the lateral roots then function as the lateral roots of the accessory system.

Accessory bundles are also found at a higher level in the shoots, both normal and reproductive, but they arise quite independently of the accessory system we have described, and are small regular and inconspicuous externally. These are incorrectly described in a recent paper by Mr Sabnis (1) as anomalous cortical bundles, but as they arise inside the endodermis it is obvious that the word "cortical" is a misnomer.

DISCUSSION

The observations described in this paper make it clear that the whole development of the accessory bundle system is directed to the gradual separation of reproductive branches which will eventually become established as separate plants. So far as we are aware, such a provision for vegetative reproduction is markedly different from anything previously described. The plant is a prominent member of a psammophytic association in which a likelihood of partial burying in the sand clearly exists, and though we have not actually seen the process taking place, our observations point to this conclusion, since much diversity exists in the depth at which the transition region is met with in plants of the same age. Such a state of affairs will obviously accelerate the separation of branches initiated by the process we have described. We thus see that when the main axis of the plant perishes, a circle of branches separated to below the ground level is already established, and it cannot be doubted that the separation must eventually become complete.

The family Leguminosae is well known to be remarkable for the frequency with which abnormal or unusual vascular structure is met with, but none of the accounts of such structures indicate, so far as we are acquainted with them, that they are connected with any specialised method of vegetative reproduction, nor do we think, regarded purely as anatomical peculiarities, that the structures hitherto recorded are quite comparable with those here described. Further reference to literature would therefore appear superfluous.

It is worthy of notice that though the plant is seen flowering during the major part of the year it seldom seems to develop seeds. This season, however (November, 1920), the mature pods have been collected in large numbers, a phenomenon which we attribute to the almost complete failure of the latter half of the monsoon.

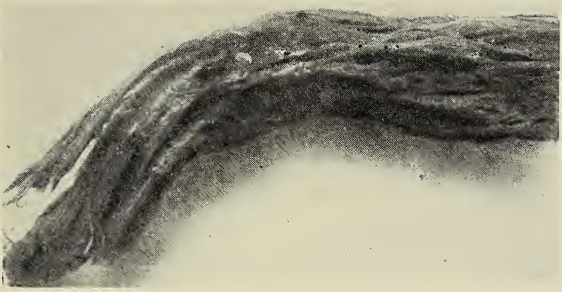


Fig. 1

Fig. 2

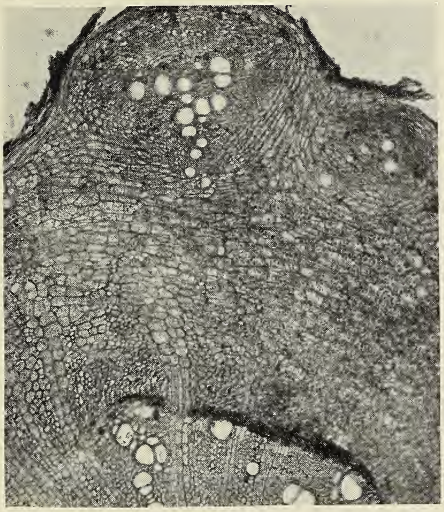


Fig. 3

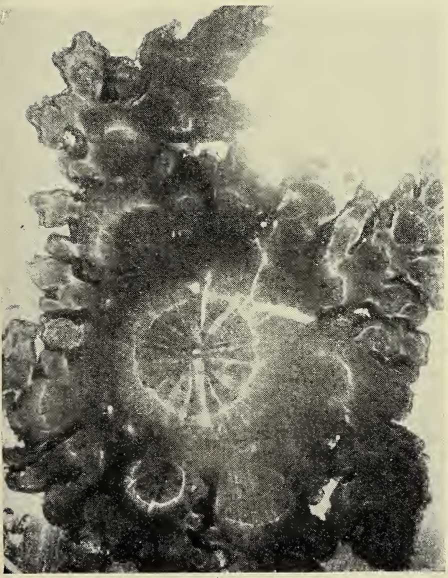


Fig. 4 *a*

Fig. 4 *b*

DASTUR AND SAXTON—VEGETATIVE MULTIPLICATION IN *CROTALARIA BURHIA* HAM.

Acknowledgment

We desire to record our indebtedness to Mr A. G. Tansley, F.R.S., for some helpful suggestions made to one of us during the progress of this investigation.

Note. This investigation was carried out in the Botanical Laboratory of the Madhavlal Rauchhodlal Science Institute, Ahmedabad.

LITERATURE CITED

(1) Sabnis, T. S. The physiological anatomy of the plants of the Indian Desert. *Journ. Ind. Bot.,* **1**, p. 197 and Fig. 101. March, 1920.

Explanation of Plate II

Fig. 1. A piece of an old root. $\frac{5}{6}$ natural size.
Fig. 2. Transverse section of a young root, showing origin of accessory bundles. $\times 160$.
Fig. 3. Older stage. $\times 33$.
Fig. 4 *a*. A thick section, almost complete, of a late stage. $\times 3\frac{3}{4}$.
Fig. 4 *b*. Part of a similar, but thinner, section, showing detail. $\times 25$.

A NEW SPECIES OF *CŒLASTRUM*

By FLORENCE RICH, M.A.

(From the Botanical Department, East London College)

In making collections of algæ from various pieces of water in Leicestershire a sample was gathered on April 26, 1915, from a very narrow ditch (choked with phanerogamic vegetation and much overhung with ivy, brambles, etc.) that bounds the garden of the large house known as Leicester Frith, situated on Boulder Clay overlying Keuper Marl, on the Groby Road, near Leicester. When this was examined it was found to contain three species of *Spirogyra*, of which *S. quadrata* (Hass.) Petit was the commonest, *Vaucheria sessilis* (Vauch.) D.C., many diatoms, and numerous small colonies of cells which proved to belong to an interesting and apparently undescribed species of *Cœlastrum*. Repeated attempts to obtain fresh supplies of material were unfortunately without success. In the original sample, however, there is a considerable amount of material available, and the organism can be observed in many different stages (of which a few have been figured).

The cœnobium of the new species of *Cœlastrum* consists of 2, 4, 8 or more, rounded cells; perhaps 8 is the commonest number. Single cells are frequent, and apart from the typical *Cœlastrum* grouping irregular colonies occur (Fig. XV). The cells vary in size from $11\,\mu$ to $14\,\mu$ in diameter.

The cœnobia are sometimes surrounded by a wide—or narrow—mucous investment with a well-defined boundary, but more often than not this investment is wanting.

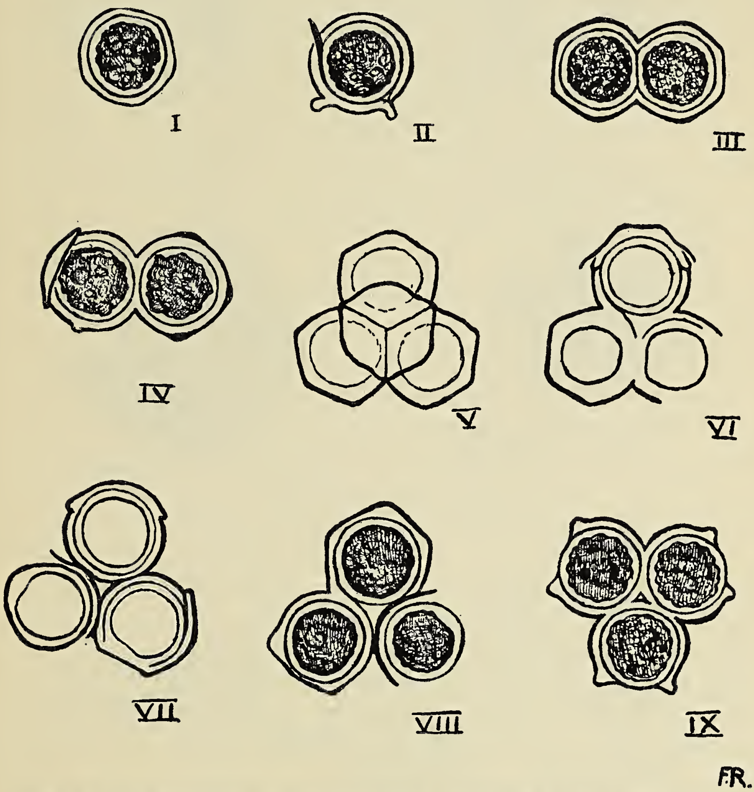
The cell-contents (in the preserved material) are light bluish green in colour, the smaller (? younger) cells showing a more yellowish tinge. The chloroplast has not been completely deciphered, but there *appears* to be one in the form of a convoluted plate. There seems to be one pyrenoid in each cell. The contents show the presence of plentiful starch.

The cell-wall is laminated and is evidently rather mucilaginous as it is penetrated by methyl blue.

Isolated cells are, roughly speaking, spherical in shape; when there are groups of two or more the cells, though still frequently

round, are very often angular. The cells that show this "rounded angularity" are quite symmetrical, triangular in optical section, with a suggestion of three other intervening angles, thus appearing faintly hexagonal (Fig. v)—like the transverse section of the ovary of *Viola*.

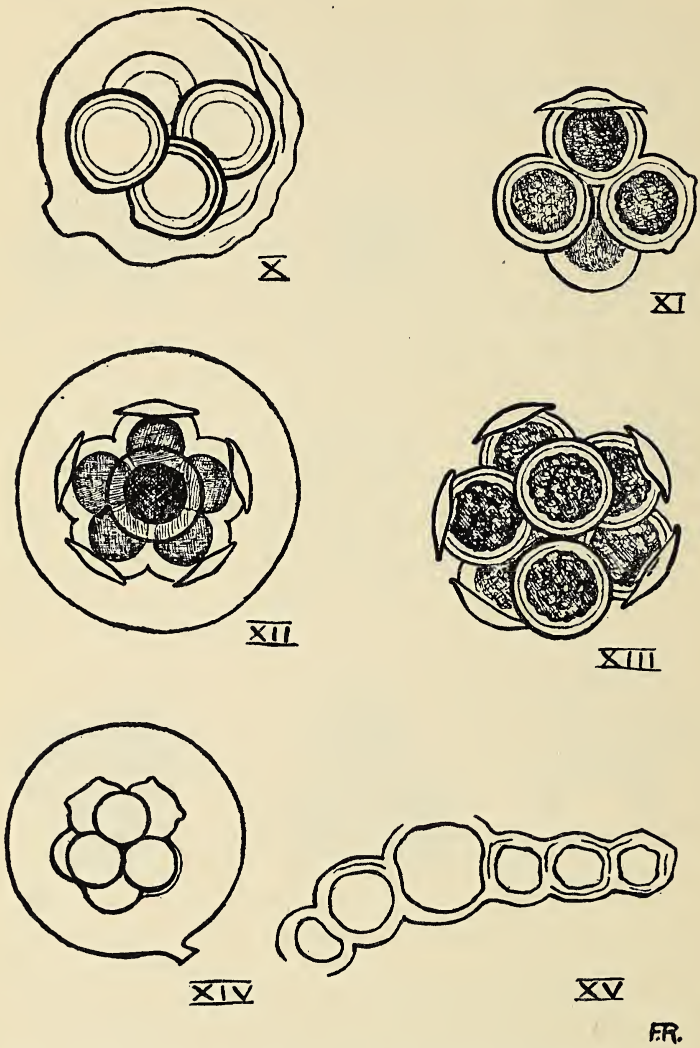
When the cells are spherical the spaces between them are very small, much smaller than in other species of *Cœlastrum* (even *C. microporum* Naeg.), and these spaces are triangular in form (Figs. VIII and IX).



Figures of *Cœlastrum schizodermaticum* (magnified about 900 times).

I. Single cell showing slight departure from spherical shape.
II. Single cell showing splitting membranes.
III. A two-celled individual showing angularity of cells.
IV. Thickening at angles, and formation of one cap.
V. Colony of four cells.
VI. Colony of four cells, one cap splitting off.
VII. Showing splitting away of outer membrane.
VIII. The same.
IX. Colony of four cells all having lost caps.

With regard to the grouping in the eight-celled families it is found that sometimes there are two superimposed tiers of four cells each,



Figures of *Cœlastrum schizodermaticum* (magnified about 900 times).

X. Four-celled colony showing connection of mucous investment with caps.
XI. A four-celled colony with a very clear and conspicuous cap on one cell.
XII and XIII. Mature cœnobia with, and without, investment.
XIV. Investment showing stalk-like protuberance.
XV. An irregular colony.

the members of one tier alternating with those of the other; sometimes, however, the *appearance* is of five cells in one plane with one cell above and two cells below (Fig. XII).

The cells of the cœnobia cohere by means of broad flattened surfaces and there are no connecting rods or tubercles.

The peculiarity of this organism is the splitting off of little cap-like structures from the free surfaces of the cells. First of all minute pads appear, about one-fifth or one-sixth of the circumference apart (Fig. IV); then fission of the outer layer of the cell-wall seems to occur along a line connecting at least two of these pads, and a little circular or four-cornered cap is detached (Figs. XI, XII and XIII). An eight-celled colony with the little caps well defined presents a very characteristic appearance. Sometimes fission of the wall occurs along the surface attached to other cells; in this case, of course, the cell in question ultimately breaks away and the cap-shaped structure is left adhering to the residue of the main colony like a little saucer (Figs. VII and VIII).

The small pads may correspond to the special short truncate processes or warts that unite the cells in other species of *Cœlastrum*, e.g. *C. Morus* W. and G. S. West, *C. scabrum* Reinsch, *C. cambricum* Archer, and *C. reticulatum* Danz. It may be the case that the cell-wall is becoming more mucilaginous at these spots, and that this causes splitting off of the caps. It is possible that the caps themselves ultimately become mucilaginous and merge into the mucilaginous envelope, as is indicated in Fig. X where folds in the investment seem to pass over into the little caps.

With regard to multiplication, the formation of auto-colonies by the cells of an entire colony has not been observed. Cases, however, like that shown in Fig. XIV would seem to indicate the possibility of formation of daughter colonies by single cells which may have been produced by disintegration of adult cœnobia, the daughter-colony being at first enclosed within the mucilaginous wall of the parent cell. The stalk-like protuberance of the investment in Fig. XIV may have resulted from the gelatinisation of one of the incipient caps.

The following Latin diagnosis is appended:

Cœlastrum schizodermaticum n.sp.

C. coenobiis globosis, tegumento mucoso interdum praeditis, e cellulis sphaericis vel subangularibus confertis, vulgo 8, constantibus, faciebus deplanatis cohaerentibus, membrana lamellata; lacunis inter

cellulas minutissimis triangularibus; lamella externa membranae saepe in forma mitrae circularis vel quadrangularis soluta est; chromatophora singula (?) in quaque cellula cum pyrenoide; multiplicitis non satis cognita.

Diam. coenob., ca. 35 μ; diam. cell., 10–14 μ.

My thanks are due to Prof. F. E. Fritsch for the generous help he has given me in studying this little organism.

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LEICESTER.

NOTES ON AN EASY METHOD OF CAMERA LUCIDA DRAWING

BY JAMES SMALL

(With 2 figures in the text)

A COMBINATION of Baker's "Reflex Drawing Apparatus" with an Ediswan "Pointolite Lamp" has proved so satisfactory in working that these notes have been written to make known the ease and speed with which a clear *camera lucida* drawing can be made by this method.

The Reflex Drawing Apparatus[1] is a small right-angled prism with the 45° side silvered (the whole protected by metal fittings), which is affixed by means of a small screw upon the top of any ordinary eyepiece. It possesses several advantages over the larger mirrors in common use. Firstly, it is small, convenient to handle, easily adjusted, and when affixed to the eyepiece it can be readily turned up so that the field may be viewed through the mirror from above. Secondly, the mirror surface is protected by glass which is exposed only to a small extent; this largely obviates the numerous cleanings necessary with the larger mirrors, and the deterioration of the surface which is a consequence. Thirdly, since the rays pass into

[1] Sold by C. Baker, 244, High Holborn, London. Price, 17*s*. 6*d*.

and out of the glass at right angles to the surface, double reflections are avoided and the reflecting apparatus becomes as efficient as a simple metallic mirror.

The "Pointolite" outfit[1] is becoming so well known, and is, indeed, so rapidly becoming one of the recognised pieces of equipment for microscopic work, that description is unnecessary. Special stands and holders for the lamp are supplied, but in the present case the lamp-holder was attached to a heavy base with a universal ball and socket joint which happened to be available. For drawing purposes the lamp is arranged in the vertical position and covered with an oblong

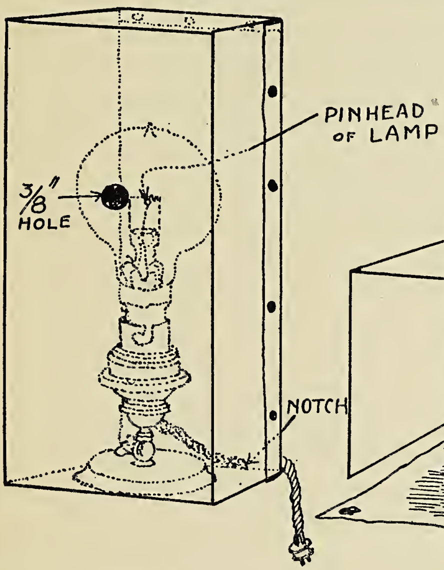

Fig. 1

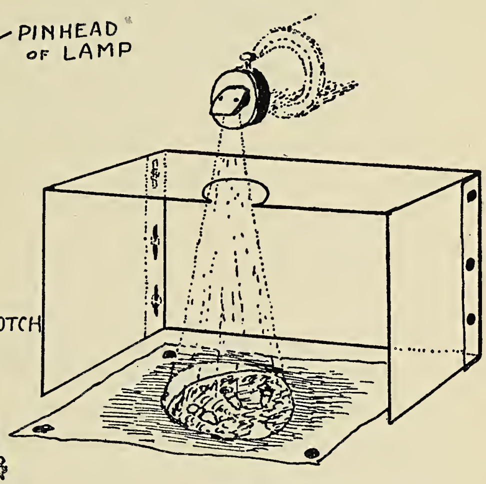

Fig. 2

case of cardboard. This case (Fig. 1) has a small notch in the base, through which the flexible wire is passed, allowing the base of the case to rest flat upon the bench. In one side of this cardboard cover and exactly on a level with the small "pinhead," which forms the source of light, a round hole not more than three-eighths of an inch in diameter is cut.

The substage mirror is removed from the microscope, or swung to one side, and the microscope is tilted into the horizontal position. The height of the tube in this particular case is slightly less than that

[1] The Standard 100 candle power lamp has been used (cost 24*s.*) with the Standard Universal Resistance Box and fittings (cost £5, less $33\frac{1}{3}$ %), as supplied by the Edison Swan Electric Co., Ponders End, Middlesex.

of the hole, and the instrument is raised by flat wooden blocks until the optical axis is on a level with the centre of the hole and with the glowing pinhead of the lamp. It is pushed as close up to the hole in the cardboard casing as the stand will allow. The section to be drawn is then inserted, and the chosen field illuminated as evenly as possible and as brightly as is compatible with clear definition of details. The Reflex Drawing Apparatus is now screwed on (the appearance of the field can be checked by turning the mirror upwards) and then the mirror is turned so that a bright, clear picture showing details and colouring as in the direct view is thrown upon paper placed flat upon the bench.

The brightness of the image upon the paper varies, of course, with the amount of light from other sources. The stray beams from the hole in the cardboard casing have little effect, if the apparatus is properly fixed up. The image is faint in full daylight, but in twilight or when dark blinds of the now usual type are pulled over the windows the image is quite bright. Final adjustments of brightness can be made easily by using (1) a half cover of cardboard (Fig. 2) which shades the image from all extraneous light[1] except from the observer's direction and his shadow acts very efficiently from that side; (2) an ordinary night-light which can be moved about until lines drawn upon the paper are visible while the image still remains clear. Nothing more remains to be done now, except to draw lines in pencil or in ink around the outlines of cells and to fill in as many other details as are required in the same way; the actual process of drawing becomes easier and more rapid than tracing with transparent paper.

The advantages of this method are—firstly, the ease with which the adjustments can be made when the apparatus *has been* in working order; secondly, the brightness and clearness and flatness of the image which make it possible to work in daytime without a dark-room; thirdly, the ease and comfort with which a *camera lucida* drawing can be made when one has the paper flat upon the bench and when both image and paper are viewed directly, and not one or other as a reflection; fourthly, the comparatively low price of the apparatus, especially when it is considered that apart from the reflex mirror the rest of the apparatus is useful for so many other illuminating purposes. The total cost is, in fact, less than that of many of the usual *cameræ lucidæ*.

[1] These cardboard cases can be made easily by ruling heavily with a blunt point the lines for folding, and then fixing the edges which overlap with split-pin paper fasteners or drawing-pins.

One of the great difficulties in making drawings of consecutive portions of a large section is that the end of one portion only fits exactly to the beginning of the next portion when the plane of the drawing paper has been very accurately adjusted in the same plane as the object or the image. Using this method, one can move the section by hand or on the mechanical stage and leave a part of the section already drawn still in the field. This part can be fitted easily on to the drawing by moving the latter in the direction followed by the moved image. The outlines of both are clear and can be superimposed quite accurately and easily, and then the drawing of the new portion can proceed. These adjustments only involve the turning of the mirror into the correct plane and this can be done rapidly, because it is only necessary to get a circle of light and not an ellipse. If two diameters of the illuminated zone at right angles to each other are equal the adjustment of the mirror is accurate.

As examples of diagrams drawn in pencil or directly in ink by this method in from two to ten minutes readers are referred to my *Textbook of Botany* (Figs. 148, 150, 270 *a*, 395, 399, 400), while for detailed drawings occupying never more than one hour, and sometimes only fifteen minutes for the pencilling, they may note the Figures 149, 151, 153, 154, 157, 268, 270 *b*, 274, 308 and 396 in the same volume.

BOTANICAL DEPARTMENT,
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AN UNUSUAL PLANT OF *CHEIRANTHUS CHEIRI* L.

By ETHEL M. POULTON, M.Sc.
University of Birmingham

(With 16 figures in the text)

In May, 1921, the writer observed a curious plant of *Cheiranthus cheiri* growing in the garden of Merion Lodge, Hagley, Worcestershire. On examination, the plant was found to exhibit interesting deviations from the usual structure.

Though the inflorescence was of the normal racemose type the general appearance of the plant was quite unlike an ordinary wallflower. This was partly due to the inconspicuous nature of the flowers. The petals were greenish-yellow, simple in shape, showing no differentiation into limb and claw, somewhat concave, and much reduced in size. Indeed, they were smaller than the sepals and therefore almost enclosed by the calyx (Figs. 1, 1 *a*). The sepals were of the typical shape, size and number (2 + 2; 2 saccate), but were inclined to be petaloid. Their margins and apices were usually yellowish. The flowers gave the impression of unopened flower-buds rather than mature specimens. Sepals and petals had dropped from the oldest flowers, but no fruits appeared to be forming. This circumstance may probably be correlated with the absence of an attractive corolla. Self-pollination could not occur for reasons which follow.

The most striking feature of the flowers was the entire absence of functional stamens and their replacement by carpels in various stages of development, a stigma and minute ovules being formed in many cases. The characteristic number (6) was everywhere preserved, and often the usual arrangement (2 + 4) could be observed. Another curious feature was the tendency of the rudimentary carpels to fuse with the central gynæcium forming a composite structure (Figs. 2, 3, 6, 11, 13)[1]. This fusion was partial or complete, both as regards individual "staminate carpels" and the whorl as a whole. Where such fusion occurred the seam was usually well marked. The car-

[1] In Figs. 2, 3, 6, 10, 11, 12, the calyx and corolla have been removed.

pellary nature of these structures was shown in one or more of the following ways:

(*a*) An incurving of the margins, along which minute ovules were formed (Figs. 7, 9);

(*b*) the formation of a stigmatic surface, often swollen but always covered with minute excrescences as in the typical stigma (Figs. 7, 8, 11, *sg*);

(*c*) the outer surface was pale green and covered with a fine down as in normal carpels.

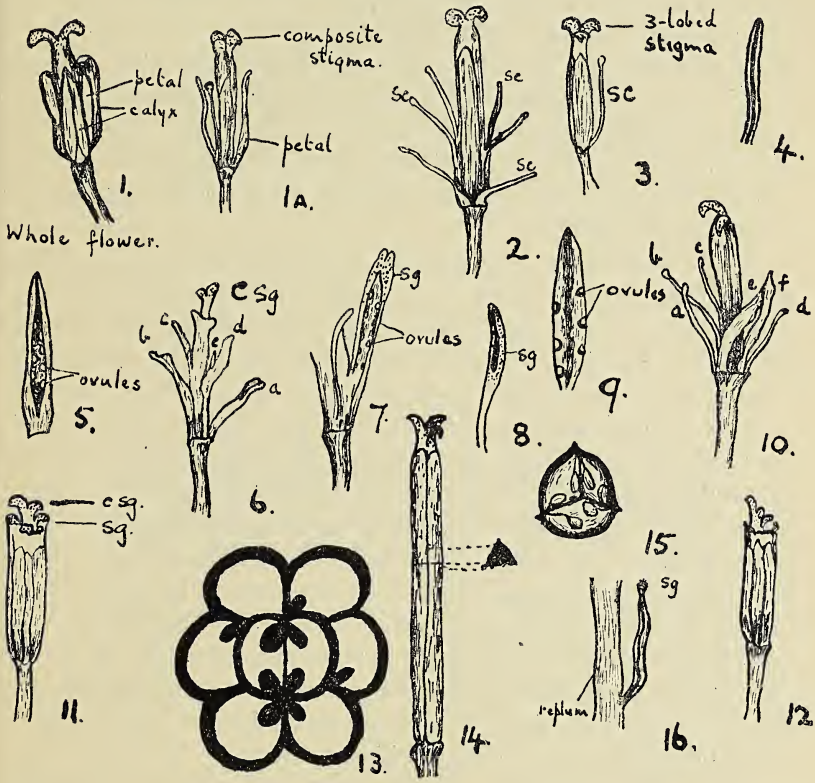

Fig. 2 shows six "staminate carpels" (*sc*) joined to the normal central gynæcium only at the base, the upper parts being free. The central gynæcium is of the ordinary wallflower type. In Fig. 3 is seen a 3-lobed stigma in the centre of the flower, one free "staminate carpel" (*sc*), the others having fused with the wall of the central gynæcium. Fig. 4 shows a petal with the edges curling towards each other, while Fig. 5 represents a "staminate carpel" from the same

flower, with the margins closing over and forming small ovules. The remaining parts of the same flower (after the removal of calyx and corolla) are seen in Fig. 6. The central stigma, *csg*, is 2-lobed, *a–e* are "staminate carpels" all of which are joined at the base; *a* and *b* tend to curl over at the tip, and produce minute ovules in various stages of development. Each also has a distinct stigmatic surface. Fig. 7 is an enlarged view of *b*, showing the ovules, and the stigmatic surface *sg*.

In Figs. 8 and 9 are seen "staminate carpels" from other flowers.

Fig. 10 represents four barren "staminate carpels" (*i.e.* without ovules) *a–d*, and two better developed ones *e*, *f*, which unite with each other and with the base of the main gynæcium. These (*e*, *f*) had rudimentary ovules on their margins. In Fig. 11 the union is almost complete, a solid column being formed of the central gynæcium and the six "staminate carpels" the stigmas (*sg*) being separately recognisable. The normal 2-lobed stigma, *csg*, is seen projecting from the surrounding stigmatic surfaces (*sg*). Fig. 12 shows the same flower rotated through 90°.

A cross-section of this composite gynæcium is shown somewhat diagrammatically in Fig. 13. The main gynæcium is seen in the centre and is of typical structure. The six "staminate carpels" have completely fused with it. The plane of the section has passed through some of the ovules formed by these.

Thus, the suppression of maleness, as regards its ordinary manifestation is complete throughout the whole plant, and the tendency to femaleness is strongly marked. It is possible that even the corolla shows this tendency in the curling over of the edges of some of the petals (Fig. 4). Very significant is the preservation of the characteristic number and arrangement of the stamens, as though the primordia of these had been formed as usual. It is difficult to resist speculation. Perhaps one might hazard the suggestion that an absence of the factor (or factors) making for maleness, or a preponderance of that (or those) associated with femaleness, might account for these curious divergencies from the familiar structure.

Worsdell (1) describes a similar abnormal flower of *Cheiranthus cheiri* and states that it is an example of "carpellody" which "is a frequent phenomenon revealing to us the fact that the stamens and carpels are very closely allied organs, and the facility with which the one may change into the other, doubtless due to the fact that both are derived from a common ancestor, the asexual sporophyll which exists to-day in some of the more primitive types of plants such as ferns, horse-tails, and some lycopods." (2)

Masters (3) states that de Candolle mentions such a plant in his *Prodromus* as a distinct variety under the name of *gynantherus*. A description of a similar flower by Brongniart (4) is quoted. This, however, differs in some details from the case described above. The "staminate carpels" were in some cases fused into two lateral bundles of three each, and in many instances the two outer stamens were entirely suppressed. He states that the two shorter stamens undergo change into carpels later than the longer ones, a point which the above specimen did not illustrate.

Addendum

Figs. 14–16 are taken from a different wallflower plant, growing in the vicinity of the one described above. They represent the gynæcium of the only abnormal flower in the whole inflorescence. The peculiarity here is the 3-carpellary ovary with a 3-fid stigma (Fig. 14). In the section, three partition walls are seen dividing the ovary into three chambers. At the base of the ovary, arising from the septum was an out-growth resembling a "staminate carpel" of the above specimen (Fig. 16). The edges were folded inwards, the outside was downy, and the tip was covered with the minute excrescences characteristic of the typical stigma.

REFERENCES

(1) *Principles of Plant Teratology* (Ray Society), 2, p. 184.
(2) *Op. cit.*, p. 182.
(3) *Vegetable Teratology* (Ray Society), pp. 305–6.
(4) *Bull. Soc. Bot. France*, 8, p. 453.

THE THEORY OF GEOTROPIC RESPONSE

By V. H. BLACKMAN

I HAVE read with some surprise Prof. Small's reply in this Journal (**20**, pp. 73–81, 1921) to my criticism of his theory of geoperception. I understood that the cell particles which "creamed" were the ultramicroscopic disperse phase of the protein sol of the protoplasm, a view which I find was taken generally by botanists. Prof. Small now tells us that we are all mistaken in our interpretation and that the theory applies to the much larger visible particles of the granular protoplasm. The basis of this misunderstanding appears to be the author's somewhat peculiar application of the term "disperse phase." On his assumption protoplasm consists of an "emulsion of protein or protein-lipoid particles in a colloidal protein medium." The system postulated has thus two disperse phases; the author, however, applies the term "disperse phase" solely to the particles, and neglects altogether the disperse phase of the protein sol, to which on the ordinary colloidal theory the special properties of protoplasm are due. It is, therefore, not surprising that confusion has occurred, especially as references to iso-electric points naturally lead one to believe that protein sols are being considered. His scientific colleagues can, I think, with some justice complain of the vagueness of outline and the lack of detail in the picture which Prof. Small presented to them. Apart from the difficulty of interpretation just mentioned, such important points as the size of the particles which were to react, the rate at which they were to move, and the extent to which redistribution would take place, were all left quite untouched although they were fundamental to the theory.

The theory has now assumed such a different complexion that it would seem unnecessary to refer to Prof. Small's misunderstanding of some of my criticisms. What is now required is direct evidence of "creaming[1]." There might be some excuse for the publication without such evidence of a theory based on the movement of ultra-

[1] The rate of movement of the large particles cannot be deduced directly from Stokes's well-known equation for, *ex hypothesi*, the particles are producing a difference of potential. They are, therefore, doing work and their movement will thus be retarded, and possibly markedly so.

microscopic particles, but if the theory was from the first one which included the movement of *visible* cell granules an attempt to obtain direct evidence before putting forward the theory would seem more in accordance with the accepted canons of scientific procedure. The examination of meristematic cells with the microscope horizontal should soon supply proof as to whether the cell granules do, or do not, markedly "cream"; and the use of an electric field should accelerate their movement and also decide as to the nature of their charge. Until evidence of movement is available it would seem useless to discuss further the many difficulties which are still implicit in the theory.

THE HYDRION THEORY OF GEOTROPISM

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With regard to Professor Small's Hydrion differentiation theory of geotropic response, surely there is a difficulty in the electrical assumptions which has so far escaped notice.

Let us grant for the moment that the creaming process in which various particles rise through the effects of gravity might lead to the production of potential differences. It is still not clear how any current would result even so. For let us consider, for simplicity, one cell in the root, instead of a series of cells. In this cell, we will suppose that there are free positively charged particles, which tend to rise under gravity. This they will do, then, until the forces on them due to gravity are balanced by the electrostatic attractions between them and the relatively negative remainder of the cell. At this point equilibrium will be reached, and there can be no current unless there is a return path for discharge. To suppose that a current will be produced in the reverse direction down the cell is equivalent to supposing that when a Voltaic cell is set up with terminals unconnected, the production of positive and negative poles will cause a reverse current to flow from positive pole to negative *in the cell*!

Professor Small says that Bose has found in stems and roots currents of the required kind. Now it is true that when Bose connects

through a galvanometer two points in a tissue at different potentials, he finds that a current flows round the circuit, but this does not show that the same current was flowing before the circuit was made. Moreover, when the current does flow, since it flows from positive to negative in the wire, it must flow from negative to positive in the tissue, just as in the Voltaic cell, when on closed circuit, the current in the cell flows from negative to positive pole, being forced up against the potential gradient by the internal forces of the cell. Thus in the tissue, when a current is artificially produced, it will flow in the opposite direction to that required by Professor Small. This point of view is in agreement with that of animal physiology, and also of Bose in his *Comparative electro-physiology*, though it is true that in earlier writings (cf. *Plant response*, p. 33) he found some objection to it. But it is of no use to go further into the question of direction of current, until it is made clear what bearing the question has upon Professor Small's theory. On this point we have only his brief statement that a downward flowing current in the root will produce greater effect at the lower side "on account of the resistance in the circuit." (This Journal, **19**, No. 3, p. 53.) As I suspect that others besides myself have been puzzled by this statement, may I ask for further explanation?

But the chief source of difficulties is surely the practice of speaking of "currents" in tissues when the evidence only shows that there are potential differences. There appears indeed to be no direct test for currents in tissues in a state of nature, though it is evident that such must occur, by local short-circuiting through cell walls or other paths.

Such currents must, in fact, occur if the two points at different potential are connected also by tracts of conducting tissue other than those along which the forces are acting which produce that potential difference: but then the resulting currents will be circular, flowing in one direction along the one path and in the other direction along the other.

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